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THE
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NORMAL AND PATHOLOGICAL,
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CONDUCTED BY

SIR WILLIAM TURNER, M.B., LL.D., D.C.L., D.Sc., F.R.S.,
PROFESSOR OF ANATOMY IN THE UNIVERSITY OF EDINBURGH;

D. J. CUNNINGHAM, M.D., D.Sc., LL.D., D.C.L., F.R.S.,
PROFESSOR OF ANATOMY AND CHIRURGERY IN THE UNIVERSITY OF DUBLIN

A. MACALISTER, M.D., F.R.S.,
PROFESSOR OF ANATOMY IN THE UNIVERSITY OF CAMBRIDGE;

J. G. M'KENDRICK, M.D., LL.D., F.R.S.,
PROFESSOR OF THE INSTITUTES OF MEDICINE IN THE UNIVERSITY OF GLASGOW;

AND

G. D. THANE,
PROFESSOR OF ANATOMY IN UNIVERSITY COLLEGE, LONDON.

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Journal of Anatomy and Physiology.

TOPOGRAPHICAL SKETCH OF THE LATERAL WALL OF THE PELVIC CAVITY, WITH SPECIAL REFERENCE TO THE OVARIAN GROOVE.¹ By WM. WALDEYER, M.D., Sc.D. Dublin, *Professor of Anatomy, University of Berlin.* (PLATE I.)

INTEND to give some account of the topographical anatomy of the outer wall of the pelvic cavity, especially with regard to the ovarian groove (*Fossa ovarii*), and to the position of the ovary.

If we look on the inner lateral wall of the pelvic cavity, we can see in the male pelvis, without any dissection—except a large amount of subperitoneal fatty tissue be present—the following topographical arrangements.

On the side of the bladder we shall find, when this organ is empty, a groove or depression, which I shall call '*Fossa paravesicalis*.' This groove is limited in front by the upper margin of the pubic bone, and behind (viz., in the male) by the vas deferens. A very well defined peritoneal fold, which I have called the '*Plica vesicalis transversa*,' divides this groove into two—the '*Fossa paravesicalis anterior*' and the '*Fossa paravesicalis posterior*' (Fig. 1, *F. prv. a.*, *F. prv. p.*). These two fossæ are traversed by the remains of the hypogastric artery (*Arteria umbilicalis* of the German anatomists) in the upper part, and by the branches of the *Arteria vesicalis superior* below.

Immediately behind the *Fossa vesicalis posterior* there can be seen another fossa of triangular shape. It is limited above by the external iliac vein, in front by the vas deferens, and behind by the ureter.

Behind this fossa the distribution of the internal iliac vessels (*Vasa hypogastrica* of the German anatomists) will be seen.

¹ Read at the meeting of the Anatomical Society of Great Britain and Ireland, Dublin, June 9-11, 1897.

I call the triangular fossa the '*Fossa obturatoria*,' because it is traversed by the obturator nerve and vessels, and because its floor is formed by the internal obturator muscle. Moreover, in this groove you can see the Arteria umbilicalis (German nomenclature), and sometimes a vesical vessel.

The arrangement of this nerve (viz., the obturator nerve) and the vessels is as follows: The uppermost of all is sometimes the Arteria umbilicalis, sometimes the obturator nerve; but this nerve is always situated deeper in the groove than the artery; in this manner it lies on the lateral side of the artery at the point where they cross each other. Below you see the obturator artery, and lastly, the vein. (Fig. 3.)

A third fossa, farther back, in which you see the *Vasa hypogastrica* (German nomenclature—internal iliac vessels of the British anatomists), and the branches of these, may be called '*Fossa hypogastrica*.'

In the female body the arrangement of these parts is the same, but instead of the vas deferens we shall see the round ligament of the uterus.

Fig. 1 shows the position of all these parts in the female (right side). The body of a young girl of about 14 years, but well developed, was divided in the mesial plane. One sees the symphysis ossium pubis (*Sy.*), and behind the symphysis the bladder (*Ves.*). From the latter to the outer wall of the pelvis runs the Plica vesicalis transversa (*Pl. v. tr.*), which divides the Fossa paravesicalis anterior (*F. prv. a.*) from the posterior (*F. prv. p.*). The latter is crossed by the hypogastric artery (*A. umb.*). The ligamentum teres uteri forms with the external iliac vessels (*A. V. il. ext.*) and the ureter (uret.) a spacious trigonal fossa, which is the same as the Fossa obturatoria in man, and we shall call it also '*Fossa obturatoria*' in the female.

The Fossa obturatoria in the female body is occupied by the broad ligament of the uterus, the Fallopian tube (*Tub.*) and the ovary covered by the broad ligament (mesosalpinx) when this is regular. The letter '*a*' indicates the upper (hinder) angle of this trigonal fossa.

Behind and below the ureter we have, in the same manner as in man, the Fossa hypogastrica (*F. hyp.*).

I should think, that the distinction and notice of this fossæ

might have some importance in surgery, and likewise the consideration of the transverse fold of the bladder, because it clearly indicates the place of the bladder, even though the latter should be quite empty.

I now come to the '*ovarian groove*' and to the position of the ovary.

You know, that about thirty years ago *Claudius*,¹ Professor of Anatomy at *Marburg*, has first spoken of a special groove for the ovary, which he called '*Fossa ovarii*.'² He says (l.c., p. 250),—

"Weiter lateralwärts ruht das Ovarium, die lange Axe horizontal, oder meistens nach aussen ein wenig erhaben, in einer seichten Grube, der *Fossa ovarii*, die in ein fetthaltiges Bindegewebe ausgetieft ist, welches am oberen Rande des *M. pyriformis* die zum Durchtritt der *Vasa* und des *Nervus glutæus superior* bestimmte Grube ausfüllt. Seine Vorderseite wird von der *Ala vesperilionis* ganz bedeckt, so dass die Därme den Eierstock nirgends berühren; die *Tuba* läuft dicht oberhalb seines oberen Randes nach aussen und biegt sich dann abwärts hinter das Ovarium, so dass das *Infundibulum* in der lateralen Hälfte der *Fossa ovarii*, zwischen dem Grunde der Grube und der Hinterseite des Eierstockes, eingeschlossen ist."

The description of *Claudius*, as we shall state afterwards, is not exact as regards the position of the fossa, and has been overlooked by the most of anatomists. So far as I know, *W. Krause*³ was the next after *Claudius* to mention the '*Fossa ovarii*,' and he has described it more precisely. Afterwards I have given a brief notice of it,⁴ which was followed by a more exact and complete description in my paper published in the year 1892.⁵

Meanwhile appeared the '*Thèse*' of *P. Vallin*,⁶ which gives a detailed exposition regarding the *Fossa ovarii*, and the position of this organ.

¹ *Claudius, M.*, Ueber die Lage des Uterus. *Zeitschrift für rationelle Medicin*, herausgegeben von *J. Henle* und *C. v. Pfeufer*. Dritte Reihe, xxiii. Bd. S. 248, 1865.—Unfortunately this paper is left out in the Index to the vol. xxiii.; hence it is necessary to bear in mind the page 248.

² (Therefore '*Fossa Claudii*' of some German authors.)

³ *Krause, W.*, Handbuch der menschlichen Anatomie. (IIIte Aufl. des Handbuches von *C. Krause*). Bd. II., Hannover, 1879, p. 510.

⁴ *Waldeyer, W.*, Die Lage der inneren weiblichen Beckenorgane bei Nulliparen, *Anatomischer Anzeiger*, 1886, p. 42.

⁵ *Waldeyer, W.*, Beiträge zur Kenntniss der Lage der weiblichen Beckenorgane. Bonn, 1892, Fr. Cohen.

⁶ *Vallin, P.*, Situation et Prolapsus des ovaires. *Thèse de Paris*, 1887, 4. G. Steinheil.

Further, we must point to the observations of *His*.¹ He says (p. 145),—

“Da sich die Behauptungen von *Claudius* über die Stellung des Ovarium als unhaltbar erwiesen haben, so sind wir nicht mehr berechtigt von einer Fossa ovarica² [*Claudii*] zu sprechen. Die grosse Mehrzahl der Lehrbücher vermeidet auch diese Bezeichnung. *Waldeyer*, welcher sie noch gebraucht, steht hinsichtlich seiner Auffassung auf dem oben präcisirten neuen Standpunkte.³ Die von ihm ins Auge gefasste Fossa ovarica kann somit nach Ort und nach Richtung mit der *Claudius*' schen Grube nicht übereinstimmen.”

These observations and the fact, that the term ‘Fossa ovarii’ is not admitted in the number of the ‘Nomina anatomica,’ show that many anatomists do not yet consider the Fossa ovarii as a normal feature.

In the last year, 1896, however, I demonstrated, at the meeting of the ‘Anatomische Gesellschaft’ at Berlin, two preparations, each with a very well marked Fossa ovarii: in one of these the fossa was so deep, that it was not possible to see the ovary lying in the groove. I think that this was a case of a beginning *Hernia ovarii ischiadica*, such as has been described by *Schillbach*.⁴

Recently *Nagel*⁵ has adopted my views of the Fossa ovarii, but I cannot agree with him when he says (l.c., p. 8),—

“Die die Nische (viz., Fossa ovarii) umrahmenden Gefässe liegen so eng aneinander, dass der Eierstock nur durch einen ungewöhnlich gesteigerten Druck in die Grube hineingepresst werden kann.”

Lastly I point to the interesting paper of *A. Martin*.⁶ The author does not deny, it is true, that sometimes the ovary is situated in a fossa or groove, but he describes, if I have rightly

¹ *His*, W., Die anatomische Nomenclatur. Nomina anatomica. Leipzig, Veit & Comp. 1895. Separatausgabe und als Supplement zum Jahrgang 1895 des *Archivs für Anatomie und Physiologie*.

² *Claudius* has proposed the term ‘Fossa ovarii.’

³ *His* alludes here to the vertical direction of the axis of the ovary, and to other points of the topographical anatomy of this organ.

⁴ *Schillbach*, *Hernia ischiadica ovarii dextri*. *Jenaische Zeitschrift für Medicin und Naturwissenschaften*. Bd. I. S. 242, 1864.

⁵ *Nagel*, W., Die weiblichen Geschlechtsorgane. Handbuch der Anatomie des Menschen, herausgegeben von K. v. Bardeleben. Jena, 1896.

⁶ *Martin*, A., Lage und Bandapparat des Eierstockes. Festschrift für Carl Ruge. Berlin, 1896, 4. S. Karger.

understood him, this groove in another way than I have done : the ovary should usually lie more behind in the pelvic cavity as it was found by myself.

I will go no farther in this brief historical sketch, and I might for this refer to Professor *Martin's* paper, in which the literature of the topography of the ovary, and especially the question of the *Fossa ovarii*, is discussed sufficiently.

But one might easily see, that the question, if the *Fossa ovarii* is a normal human feature or no, is now open, and that it would be necessary to give a more detailed account of the position and relations of this groove than has previously been done.

Since the last meeting of the 'Anatomische Gesellschaft' at Berlin (1896, April) I have investigated more than fifty female bodies ranging from early childhood to advanced age, and I have found that the ovary is situated normally in the manner which was first pointed out by *Wm. His* and *B. Schultze*, viz., that the organ lies on the lateral pelvic wall, and vertically when the woman takes the erect posture ; the one end, the '*Tubenpol*,' near the external iliac vein, the other end, the '*Uterinpol*,' downwards, and that the Fallopian tube overlies the ovary in such a manner as to cover it on its medial face entirely, or nearly so. (Fig. 1.) The convex or free margin of the organ (*Or. II.*, Fig. 1 and Fig. 2) looks more downwards toward the pelvic cavity and behind toward the rectum, the straight margin or hilum lies laterally on the pelvic wall, attached to the mesosalpinx ; this margin is not to be seen in Fig. 1, but you see it very well in Fig. 2, *Or. III.* (*Or. I.* in the same figure indicates the ovary as a whole).

To the hilum and to the Fallopian tube are going the vessels of the ovary enveloped by their peritoneal fold ; and in my former papers already quoted I have called this fold, together with the included vessels, the '*Ligamentum suspensorium ovarii*,' Fig. 1, *Lj. susp. ov.*

Moreover, I have found that the ovary often lies in a shallow, but very distinct groove (*F. ov. I.* and *F. ov. II.*, Fig. 2) ; this groove is situated in the *Fossa obturatoria*, and therefore, as I think, more in front and higher, than it was described by *Claudius*, *W. Krause*, *Martin*, and perhaps also by *Vallin*. This fossa for

the ovary, which I have to describe, occupies a considerable part of the Fossa obturatoria, and is limited above by the umbilical (hypogastric) artery, and below by the ureter in such a manner, that the ureter goes along the convex margin of the ovary, and the umbilical (hypogastric) artery passes near the hilum, viz., the straight margin.

When the ovary is lifted from its groove, one can see very clearly the groove and its limits (see Fig. 2).

Fig. 3 shows the great iliac vessels denuded of their peritoneal covering, this latter lifted away by a little anatomical hook (ss.) from the ovarian groove. The ovary is shining through the thin peritoneal lamella. You may see in this manner also the structures which occupy the floor of the ovarian groove: first, along the external iliac vein a little lymphatic gland (*L. gl.*); then in a deeper plane, the obturator nerve, which is followed below and crossed more forward by the umbilical (hypogastric) artery. From this artery arises a little artery to the bladder (*Ram. ves.*), which crosses the obturator vessels (*V. obt.*, *A. obt.*). The vessel, which we call in Germany 'arteria umbilicalis' (hypogastric artery of the British anatomists), has often, as in the case of Fig. 3, a common trunk with the uterine artery (*A. uter.*). The latter runs together with a vein along the ureter (*uret.*), all these three following the lower border of the Fossa ovarii.

This is the position of the ovarian groove and of the ovary in this groove, which I have found in the majority of the bodies of healthy adult women, and I might hence consider this groove, which is a part of the great triangular obturator fossa, as a normal feature of the human body. I can say, further, that it is not the ovary only which forms this groove, because the groove is often marked also in the male body, although not so clearly as in the female, and because one can see the fossa in young children, the ovaries lying still at the pelvic brim. But I think that the position of the ovary in this groove is the typical position of this organ in the healthy condition of the pelvis and the pelvic viscera.

I confess freely, that this position of the ovary is not without exception, and I might yet distinguish three other positions of this organ which can be considered also as normal: first, the

ovary is sometimes situated *downwards from the ureter*, so that this duct lies along the *straight border* or *hilum* of the ovary,—this is perhaps the position described by *Claudius* and *W. Krause*; second, the ovary may be situated *higher*, so that in certain cases it reaches the external iliac vessels, and comes into the upper or large pelvic cavity, as is the rule in the latest foetal periods and not unfrequently still in the new-born child; third, the ovary may lie *farther forwards*, but this condition is rare.

One can consider all these positions as normal, because they may exist, so far as I know, without any pathological trouble; but the 'typical situation' of the human ovary is, in my opinion, that in which the organ lies in the Fossa ovarii, which I have just described as a part of the Fossa obturatoria.

EXPLANATION OF PLATE I.

Fig. 1. Vertical median section through the pelvis of a girl aged 14 years. Right half-lying posture. The ovary and the Fallopian tube in the usual position. (The uterus is not cut in the median plane, because it was situated more in the left side of the pelvis (extra-median position).)

Cp. ad., Corpus adiposum prævesicale (fatty tissue between the symphysis and the bladder).

Sy., Symphysis ossium pubis.

F. prv. a., Fossa paravesicalis anterior (anterior paravesical groove).

Pl. v. tr., Plica vesicalis transversa (transverse fold of the bladder).

F. prv. p., Fossa paravesicalis posterior (posterior paravesical groove).

Lg. ter., Ligamentum teres uteri (round ligament of the uterus).

A. umb., Arteria umbilicalis (hypogastric artery).

Tub., Tuba uterina (Fallopian tube).

A. V. il. ext., Arteria et Vena iliaca externa (external iliac artery and vein).

Lg. susp. ov., Ligamentum suspensorium ovarii (suspensory ligament of the ovary,—a serous fold which contains the vessels of the ovary).

Uret., Ureter (ureter).

a., angulus posterior (superior) fossæ obturatoriae (the hindermost (uppermost) angle of the obturator fossa).

Pr., Promontorium (promontory).

F. hyp., Fossa hypogastrica (hypogastric fossa).

Vs. uter., Vasa uterina (uterine vessels).

Rct. tr., Rectum; sectio transversa (rectum; transversely cut).

Or. II., Margo liber (convexus) ovarii (the free or convex border of the ovary). In the normal condition the ovary is always overlapped in the manner represented in this drawing, by the Fallopian tube and the broad ligament. One might see then only the free border of the organ.

Pl. Dgl., Plica recto-uterina (Douglasi) (recto-uterine fold).

Ut., Uterus.

Exc. rectut., Excavatio recto-uterina (rectovaginal pouch; pouch of Douglas).

Rct. lg., Rectum; sectio longitudinalis (rectum; cut longitudinally).

Ves., Vesica urinaria (bladder).

Vg., Vagina.

Urethra, Urethra.

An., Anus.

Lb. mj., Labium majus pudendi

Fig. 2. The same Section.

The Fallopian tube with the broad ligament are drawn away from the ovary, and the latter is by being turned around its straight or external border (hilum) removed from its Fossa.

A. umb., Arteria umbilicalis (hypogastric artery).

Pl. v. tr., Plica vesicalis transversa (transverse fold of the bladder).

Or. I., Ovarium (ovary).

Tub., Tuba uterina (Fallopian tube).

Or. II., margo liber (convexus) ovarii (free or convex border of the ovary).

B. per. or., Bursa peritonealis ovarii — bursa ovarii, *Rauber*— (ovarian pouch). When this pouch becomes much deeper and more or fully closed (mouse, rat), it is called 'ovarian sac' (*A. Robinson*, in this *Journal*, vol. xxi. p. 169). I have also

described this pouch: see Eierstock und Ei, Leipzig, 1870.

s., Anatomical hook lifting up the Fallopian tube with the mesosalpinx from the ovary.

Fbr., Fimbriæ tubæ uterinæ (fimbriæ of the Fallopian tube).

F. ov. I., Pars superior posterior fossæ ovarii (upper and hindmost part of the ovarian fossa).

Lg. susp. ov., Ligamentum suspensorium ovarii (suspensory ligament of the ovary—see explanation of Fig. 1).

A. umb., Arteria umbilicalis (hypogastric artery).

V. il. ext., Vena iliaca externa (external iliac vein).

A. il. ext., Arteria iliaca externa (external iliac artery).

A. hyp., Arteria hypogastrica (internal iliac artery).

Uret., Ureter.

Vs. uter., Vasa uterina (uterine vessels).

A. obt., Arteria obturatoria (obturator artery).

V. obt., Vena obturatoria (obturator vein).

F. ov. II., Pars inferior anterior fossæ ovarii (lower and foremost part of the ovarian fossa).

ov. III., Margo accretus (rectus) ovarii (attached or straight border of the ovary).

Fig. 3. The same Section. The Fallopian tube, with the broad ligament (mesosalpinx) is drawn outwards with the little hook, *s.*; the part of the parietal peritoneum, which invests the ovarian fossa, is dissected off and kept away from the fossa by another hook, *ss.* The ovary, *ov.*, is shining through the thin peritoneal lamella. One sees the vessels and the ureter, which runs on the borders of the fossa and lies on its floor.

Fbr., Fimbriæ tubæ uterinæ (fimbriæ of the Fallopian tube).

V. obt., Vena obturatoria (obturator vein).

A. obt., Arteria obturatoria (obturator artery).

A. umb., Arteria umbilicalis (hypogastric artery).

Lgl. il., Lymphoglandula iliaca (iliac lymphatic gland).

N. obt., Nervus obturatorius (obturator nerve).

V. il. ext., Vena iliaca externa (external iliac vein).

A. il. ext., Arteria iliaca externa (external iliac artery).

Tr. com., Truncus communis arteriæ umbilicalis et arteriæ uterinæ (common trunk for the hypogastric and uterine arteries).

A. umb., Arteria umbilicalis (hypogastric artery).

V. uter., Vena uterina (uterine vein).

A. uter., Arteria uterina (uterine artery).

Uret., Ureter.

Ram. ves., Ramus vesicalis arteriæ umbilicalis (vesical branch of the hypogastric artery).

Fig. 1.

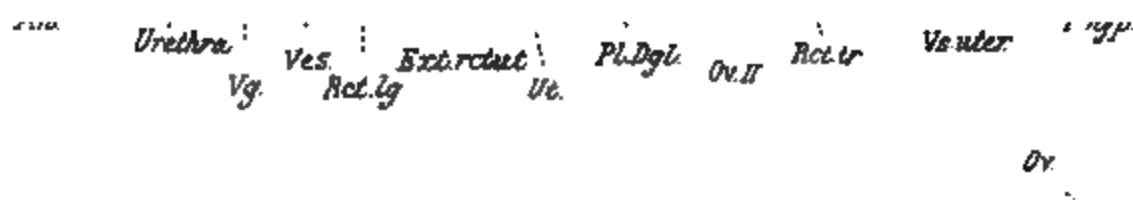
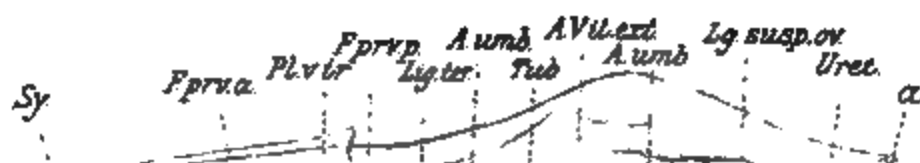


Fig. 3.



Fov. I
Fbr. La. suan. ov. Vbl. ext.

S
Fbr. Vobl. Aobl. Aumb. Lab. id.

Ov. III Fov. II Vobl. Aobl.

Ail. ext.

Tr. com.

Aumb

Iuter

Ram. ves. Uret. A. uter

THE INSULAR DISTRICT OF THE CEREBRAL CORTEX
IN MAN AND IN THE MAN-LIKE APES.¹ By D. J.
CUNNINGHAM, F.R.S., *Professor of Anatomy and Surgery*
in the University of Dublin.

MANY of the points of difference between the convolutionary arrangement of the cerebral cortex in man and in the apes, to which anatomists were formerly inclined to attribute considerable importance, have recently been found, on fuller study, to lose much of their weight, whilst others previously unsuspected and much more striking have come to light. This is largely due to an increased knowledge of the manner in which the gyri and sulci assume shape upon the developing foetal brain. It cannot be too strongly insisted upon that a just comparison of the human and simian cortex can only be undertaken by those who have rendered themselves familiar with the growth of the early human cortex. There is no region which more fully illustrates the truth of this assertion than the insular district.

In the anthropoid ape the insula or island of Reil consists of a submerged hinder part, covered by a fronto-parietal and a temporal operculum, and an anterior portion, which lies free and exposed on the surface of the hemisphere, and on the same surface-level as the rest of the frontal cortex. The exposure of this part of the cortex is due to a total absence of the frontal and orbital opercula which cover the corresponding part of the human cortex. Another striking characteristic of the anthropoid insular district is the presence of the fronto-orbital sulcus which bounds the exposed part of the insula in front, and which can be shown to correspond to the anterior limiting sulcus of Reil in man.

This interpretation of the appearances presented by the insular district of the anthropoid cortex is now very generally accepted. An overwhelming number of facts can be adduced

¹ This paper was read in July 1896 at the meeting of the Anatomical Society in Oxford. An attack of typhoid fever prevented the author from publishing it at the time.

in favour of it; and it is with the view of adding one additional and somewhat important link to the chain of evidence that this paper is written. Before entering upon this matter, however, I would wish to touch briefly upon some of the more essential points which have already been brought forward in support of the views which I have expressed regarding the differences which exist between the human and anthropoid insular districts.

The temporal and fronto-parietal opercula which are present in both man and the ape appear, as might be expected, very early in the human foetus (end of the fifth month). The temporal operculum grows more rapidly than the fronto-parietal; so that when their lips come together to form the posterior limb of the fissure of Sylvius, there is a greater extent of the Sylvian fossa covered by the temporal operculum than by the fronto-parietal. This accounts for the more oblique direction of the Sylvian fissure in the foetal brain. But at this stage a growth-antagonism between the two opercula takes place, and in this the fronto-parietal operculum proves the victor. The contiguous lips of the two opercula become in the first instance tightly pressed together; and then, as the upper operculum proves the stronger and more vigorous in its growth, the posterior limb of the fissure of Sylvius becomes gradually depressed, until it assumes the inclination characteristic of the adult. The oblique direction of the fissure in the ape would seem to indicate that the opercular growth-antagonism referred to above does not occur to the same extent, if indeed it occurs at all, in the simian foetal brain. It is probable that the greater growth-energy of the fronto-parietal operculum in man, in the later stages of foetal development and in the earlier stages of infantile growth, is due to an extension of that district of the cortex in which the centres for the skilled movements of the upper limbs reside, and also, to a large extent, of Flechsig's parieto-occipital 'association' area.

The orbital and frontal opercula of the human foetal brain are late in appearing, and very tardy in their growth. They do not begin to take shape until more than half of the Sylvian fossa has already been closed by the fronto-parietal and temporal opercula. The orbital operculum appears first, and is much more constant in its growth than the frontal operculum. The

frontal operculum, indeed, frequently fails altogether and, as is well known, it shows the greatest amount of variability in the degree to which it is developed. The form assumed by the two anterior limbs of the fissure of Sylvius depends upon the degree of development of the frontal operculum, and every anatomist is familiar with the U-form when the operculum is well marked; the V-form when the operculum is less strongly marked; and the Y-form, with a varying length of the vertical or common stem of the Y when the frontal operculum is feebly developed. In those cases where the frontal operculum is absent altogether, the single anterior limb of the fissure of Sylvius is the result. The tardy growth of the orbital and frontal opercula is exhibited by the fact that it is only in the first year of infantile life that they come into apposition with each other, and with the other two opercula, to close in the Sylvian fossa completely.

The late appearance, the slow growth, the variability of these two opercula, and also the tendency to abortive growth or complete suppression of the frontal operculum, all bespeak the fact that from a phylogenetic point of view the orbital and frontal opercula are, comparatively speaking, recent productions in the human brain; and it need cause no surprise, therefore, that they are peculiar to man, and altogether absent in the ape, except in certain rare cases where the anthropoid brain in this respect takes a slight step in advance, and points out the path over which the human brain has travelled in the evolution of the Sylvian district.

A considerable amount of variability is also observed in the Sylvian district of the anthropoid brain. The accompanying figure (fig. 1) probably shows the condition which is most commonly present.

The so-called anterior limb of the Sylvian fissure (O.S.), which in reality merely represents the anterior free edge of the fronto-parietal operculum, diverges from the anterior part of the edge of the temporal operculum, and leaves a triangular field between (I.) exposed on the cerebral surface. This field is the exposed part of the insula. The fronto-orbital sulcus (F.O.) which limits this field in front represents the anterior limiting sulcus of Reil in the human brain, and forms the front boundary of the entire

insular district. Marchand¹ suggests the very appropriate name of 'opercular sulcus' for the so-called anterior limb of the Sylvian fissure; and seeing that this sulcus cannot with truth be regarded as the equivalent of either of the anterior Sylvian limbs in man, it is well to adopt the term. It will be noticed that in the chimpanzee cerebrum figured below (fig. 1) the opercular sulcus (O.S.) falls short by a considerable distance of the fronto-orbital sulcus, and that the exposed part of the insula is continued upwards between the two sulci, on the same surface-level as the remainder of the frontal cortex.

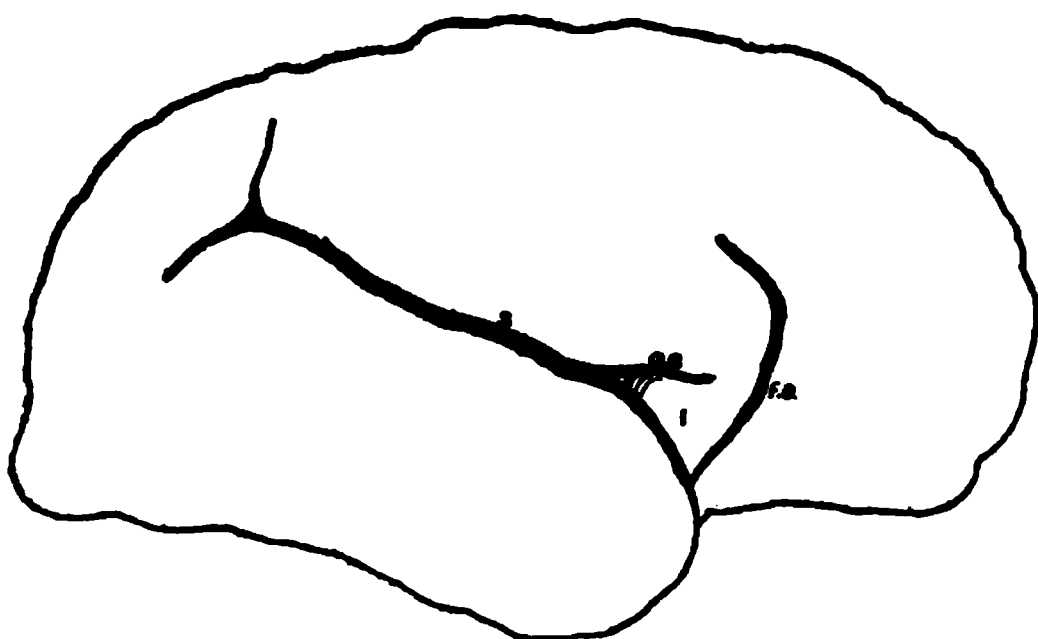


FIG. 1.—Tracing from the cerebral hemisphere of a Chimpanzee.

References common to Figs. 1, 2, 3, 4.

- S., Posterior limb of the Sylvian fissure, formed by the apposition of the lips of the temporal and fronto-parietal opercula.
- O.S., The opercular sulcus (so called by Marchand), which represents the anterior free edge of the fronto-parietal operculum.
- F.O., Fronto-orbital sulcus—the equivalent of the anterior bounding sulcus of Reil in man.
- I., The exposed portion of the insula.

In figure 2 another chimpanzee cerebrum is represented; and here it will be observed that the sulcus opercularis has made a distinct advance towards the fronto-orbital fissure. This is due to an elongation of the fronto-parietal operculum, and the immediate effect is that the exposed part of the insula is more completely cut off from the general surface of the cortex.

A further step in the same direction is seen in figure 3. The elongation of the sulcus opercularis (O.S.) has been carried

¹ Die Morphologie des Stirnlappens und der Insel der Anthropomorphen—Arbeiten aus dem pathologischen Institute zu Marburg. Zweiter Band—Erstes Heft—1893.

to such an extent that it has almost joined the sulcus fronto-orbitalis (F.O.); and this represents a very decided advance towards the condition present in the human brain, in which the entire insula is circumscribed by a limiting sulcus.

But this process may be carried to a still greater length.

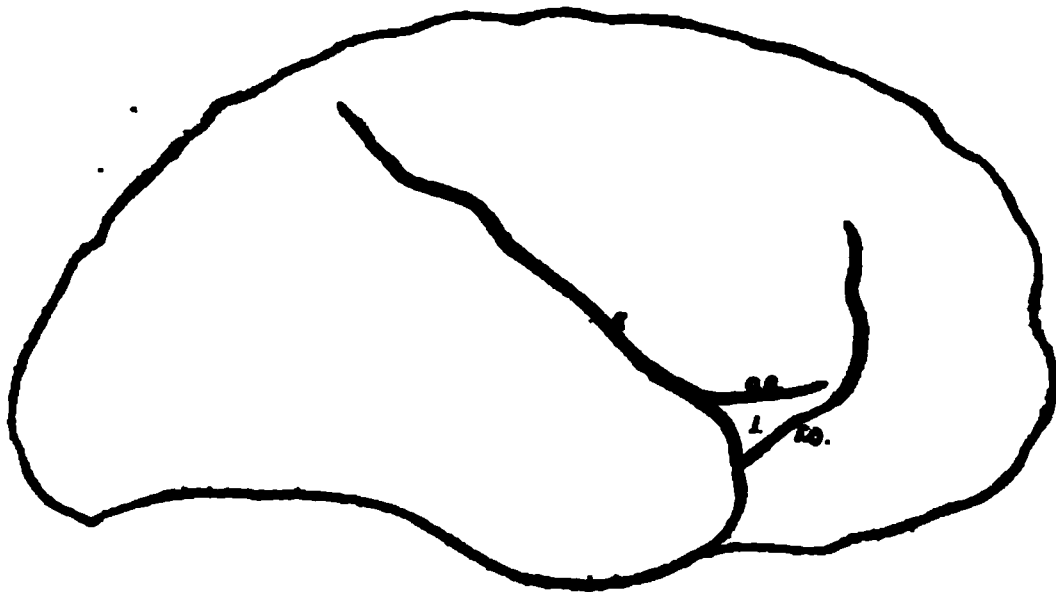


FIG. 2.—Tracing from a Chimpanzee cerebrum.

In figure 4 a union between the sulcus opercularis and the fronto-orbital sulcus has taken place. This, of course, means that the upper bounding sulcus of Reil has joined the fronto-orbital sulcus, which is the equivalent of the anterior bounding

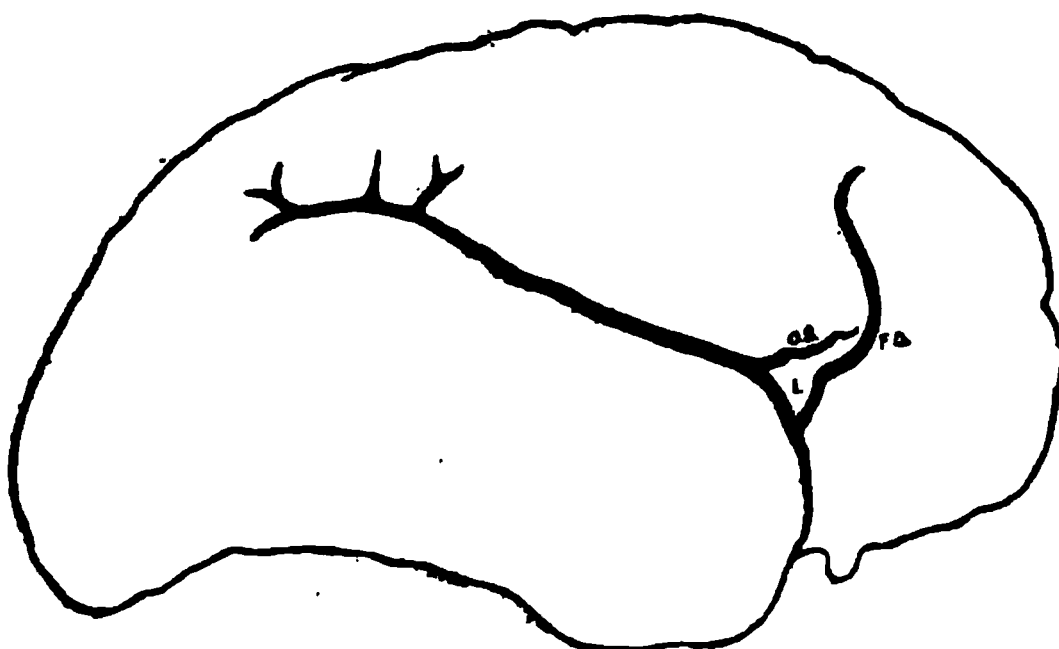


FIG. 3.—Tracing from the cerebrum of a Chimpanzee.

sulcus of Reil in man; and the insular district is in this way as completely cut off from the surrounding cortex as in the human brain. But the cerebrum from which this tracing was taken showed two further points of considerable interest, and of marked significance. The exposed part of the insula (I.) was

distinctly depressed below the general surface-level of the surrounding cortex, and the anterior lip of the fronto-orbital sulcus was very exuberant, and showed a tendency to grow backwards over the posterior lip,—foreshadowing, in this way, the formation of an orbital operculum.

This condition is rare in the chimpanzee. Still, I have in my possession photographs of two cerebral hemispheres, taken from different individuals, which show it.¹ It is also interesting to note that a similar condition of the insular district is occasionally met with in all the anthropoids. In Pansch's figure² and also in a figure by Bischoff³ of the gorilla brain it is seen; Kohlbrügge⁴ has shown that it is not uncommon in the gibbon

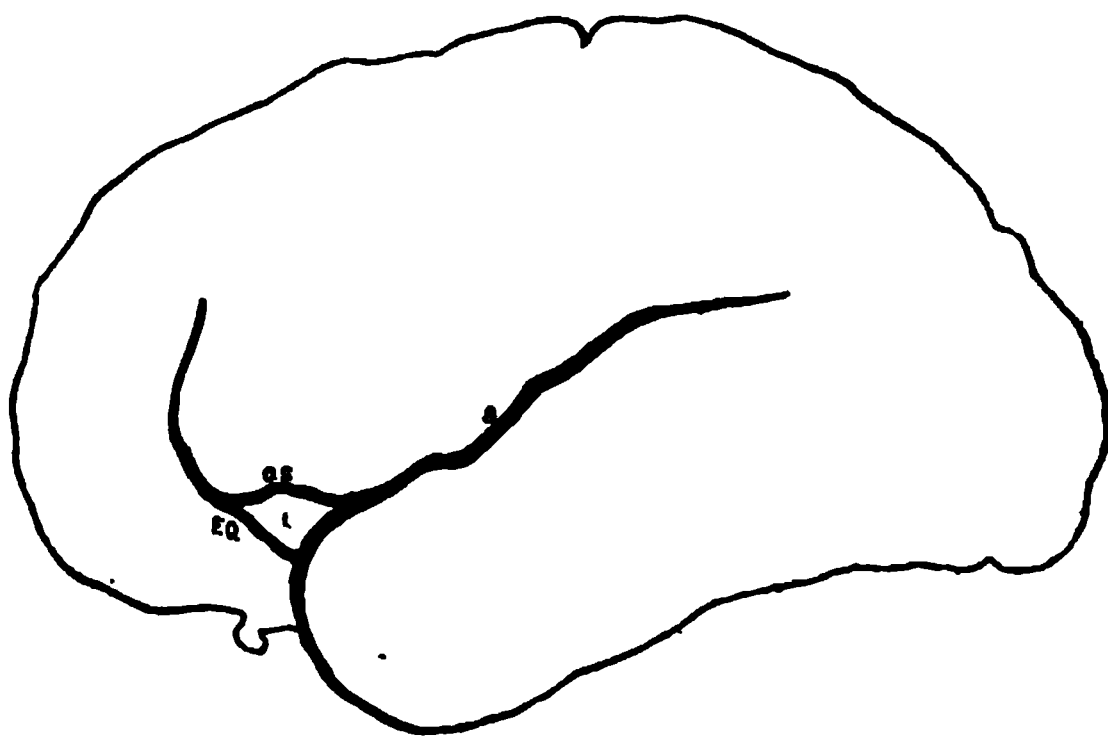


FIG. 4.—Tracing from the cerebrum of a Chimpanzee.

brain; whilst Marchand⁵ has called attention to it in the left cerebral hemisphere of an orang, and also in the right hemisphere of a chimpanzee.

The mapping out in this definite manner of the anthropoid insular district is to be regarded as a very decided advance,

¹ The second hemisphere is figured in page 19 (fig. 7).

² *Bolan und Pansch*, Abhandlungen aus dem Gebiete der Naturwissenschaften herausgegeben vom Naturwissenschaftlichen Verein zu Hamburg, 1876.

³ Ueber das Gehirn eines Gorilla und die untere oder dritte Stirnwindung der Affen. Sitzungsberichte der K. bayer. Akademie der Wissenschaften. Sitzung der math.-phys. Classe vom 10, März 1877.

⁴ "Zoologische Ergebnisse einer Reise in Niederländischen Ost. Indien," Band ii., Leiden, 1891.

⁵ "Die Morphologie des Stirnlappens und der Insel der Anthropomorphen," p. 55.

and indicates a distinct and definite tendency on the part of the brain of these apes to take a step towards the human condition. Indeed, it is not uncommon to meet with foetal brains which in the last month or so of intra-uterine development show a precisely similar arrangement of parts in the Sylvian district. Figure 5 represents a tracing from such a cerebral hemisphere. In this the frontal operculum is absent, and the upper bounding sulcus of Reil (the sulcus opercularis of the chimpanzee) joins with the anterior bounding sulcus of Reil (the sulcus fronto-orbitalis of the chimpanzee). The anterior portion of the insula is exposed, and the whole arrangement is

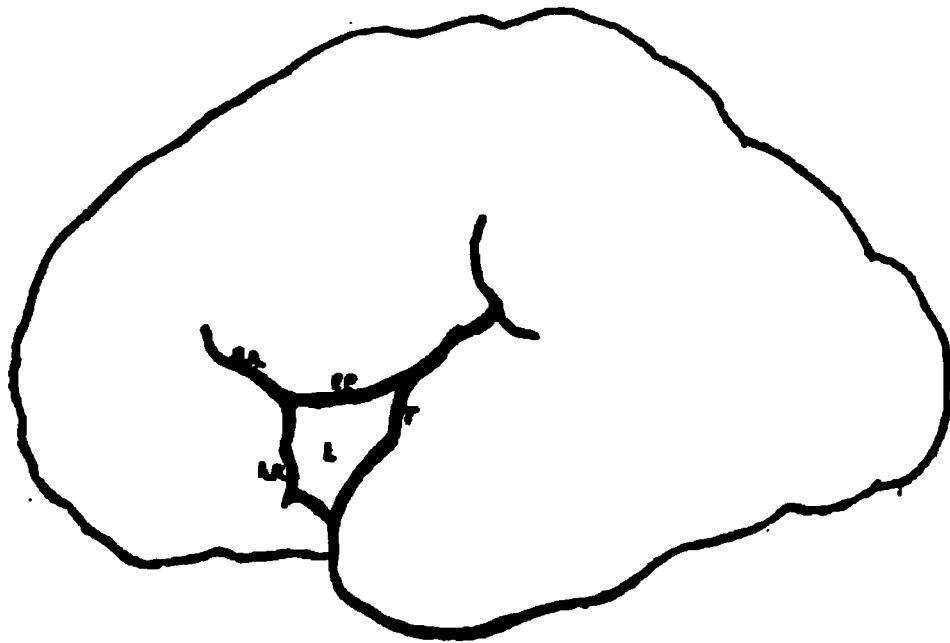


FIG. 5.—Tracing of Brain of Human Foetus at the beginning of the last month of intra-uterine development.

F.P., Fronto-parietal operculum,—the free edge below the letters forming a sulcus equivalent to the sulcus opercularis as seen in Figure 4 (O.S.) of the Chimpanzee's brain.

A.R., Anterior limiting sulcus of Reil, corresponding to the fronto-orbital sulcus in the Chimpanzee's cerebrum (*vide* Fig. 4, F.O.).

S.A., Single anterior limb of the Sylvian fissure.

to be regarded as exhibiting the early condition of parts which in the course of development leads to the formation of a single anterior limb of the Sylvian fissure, by the approximation of the lips of the orbital and fronto-parietal opercula across the space which is usually occupied by the frontal operculum (the 'cap' of Broca). From this, therefore, it will be seen that the chimpanzee and other anthropoids, when they attain the higher development referred to above, possess a true representative of the single anterior limb of the Sylvian fissure in man.

As I have already stated, the series of chimpanzee brains represented in figs. 1, 2, 3, and 4 indicate in some measure the

path pursued by the human brain in the evolution of the insular district; and it is a matter of much interest to note that the highest stage reached by the anthropoid brain (fig. 4) is practically identical with a not infrequent and low condition of the foetal human insular district.

But, to pass from this line of argument, it may be well also to state that most satisfactory corroborative evidence is afforded

L.V.
G.M.
C.N.
L.N.
I.C.
T
C.N.
P.H.
S.

FIG. 6.—Horizontal section through a left human cerebral hemisphere.

F.P., Fronto-parietal operculum.	C.N., Caudate nucleus—head and tail.
I., Insula.	T., Thalamus.
T., Temporal operculum.	I.C., Internal capsule.
C., Claustrum.	L.N., Lenticular nucleus.
S., Splenium of corpus callosum.	G.M., Genu of corpus callosum.
P.H., Descending horn of lateral ventricle.	L.V., Anterior horn of lateral ventricle.

by measurement that the submerged part of the insula of the anthropoid does not correspond with the entire insular district in man. Thus, in man the insular district forms 29·6 per cent. of the lateral length of the cerebrum; in the orang, only 21·5 per cent.; and in the chimpanzee, only 18·2 per cent. Again, it can easily be ascertained that in man 13 per cent. of the length of the insula lies in front of the coronal suture, whilst in the

chimpanzee the entire submerged part lies behind that sutural line, and in the orang the suture intersects the upper anterior corner of the insula.¹

There is still another method by which the extent of the insular district of the cortex in the anthropoid may be tested. When a horizontal section is made through the human cerebrum at such a level as to cut through the most anterior point of the island of Reil, it is seen that the area occupied by the insula very nearly corresponds with the subjacent masses of grey matter represented by the putamen and the head of the caudate nucleus (fig. 6). The extreme anterior limit of the insula corresponds very nearly to the anterior end of the head of the caudate

FIG. 7.—Right cerebral hemisphere of a Chimpanzee.

nucleus; whilst its posterior limit, as seen in a section at this level, is observed to fall slightly short of the posterior end of the putamen of the lenticular nucleus.

I have made two horizontal sections through the chimpanzee cerebrum at the levels indicated in the accompanying figure (fig. 7). The first section passed through the upper part of the fronto-orbital sulcus, and is clearly too high for comparison with the section shown in fig. 6; the second cut was made through the middle of the fronto-orbital sulcus, and corresponds in level as nearly as possible to the section through the human brain represented in fig. 6. I have reproduced the appearances presented by the cut surfaces of both sections in figs. 8 and 9.

¹ For more detailed information regarding these relations, see "Cunningham Memoir" No. vii.—Royal Irish Academy.

These sections show a number of points of extreme interest, but perhaps the most striking is the great relative size of the caudate, lenticular, and thalamic masses of grey matter in comparison with the extent of cortex. In this respect

FIG. 8.

FIG. 8.—Cut surface exposed by the higher section on the under aspect of the upper block of the cerebral hemisphere of the Chimpanzee brain, represented in Fig. 7.

FIG. 9.

FIG. 9.—Cut surface exposed by lower section on the upper surface of the lowest block of the cerebral hemisphere, represented in Fig. 7.

F.O., Fronto-orbital sulcus.	T., Thalamus.
S.L., Septum lucidum.	P.H., Posterior horn of lateral ventricle.
G., Genu of corpus callosum.	F., Posterior pillar of fornix.
L.V., Anterior horn of lateral ventricle.	S., Splenium of corpus callosum.
C.N., Caudate nucleus — head and tail.	Sy., Fissure of Sylvius — posterior limb.
P., Putamen of lenticular nucleus.	T., Temporal operculum.
A.C., Anterior commissure.	F.P., Fronto-parietal operculum.
G.P., Globus pallidus.	S.I., Submerged part of insula.
I.C., Internal capsule.	C., Claustrum.

the chimpanzee cerebrum offers a contrast to that of man: the proportion of cortical to basal grey matter in the two is entirely different. For our present purpose the section represented in fig. 9 is alone of use. In this the most anterior limit of the submerged insula (S.I.) does not extend as far forward as the anterior

end of the putamen of the lenticular nucleus, and therefore it cannot correspond with the entire area of the insula in man. On the other hand, if we take the fronto-orbital sulcus (F.O.) as indicating the front boundary of the insular region in the

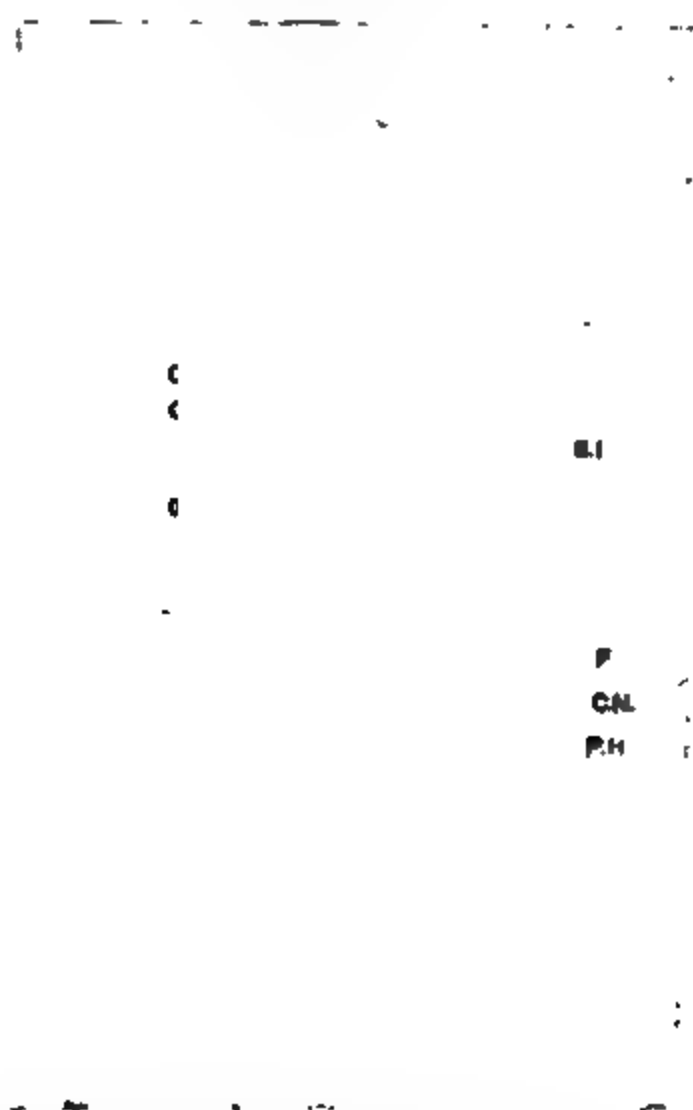


FIG. 10.—Under surface of the upper block of the left hemisphere of an Orangutan, cut horizontally across at the level of the lower section, indicated in the figure of the hemisphere of the Chimpanzee (Fig. 7).

C.C., Genu of corpus callosum.	P.H., Posterior horn of lateral ventricle.
C.N., Caudate nucleus—head and tail.	S., Sylvian fissure.
P., Putamen.	T., Temporal operculum.
F., Fornix.	F.P., Fronto-parietal operculum.
G.P., Globus pallidus.	C., Claustrum.
I.C., Internal capsule.	F.O., Fronto-orbital sulcus.
T., Thalamus.	S.I., Submerged part of insula.

anthropoid, it will be noticed that this brings forward the district to the required extent. In other words, this furrow, which, as we have stated, is the equivalent of the anterior bounding sulcus of Reil in man, corresponds in position to the anterior end of the head of the caudate nucleus.

The same result is obtained when a similar section is made through the cerebral hemisphere of an orang (fig. 10).

The submerged part of the insula (S.I.) presents an area on the surface about equal in extent to that of the outer aspect of the putamen of the lenticular nucleus, whilst the fronto-orbital sulcus cuts the cortex opposite the anterior end of the head of the caudate nucleus.

By means of Dr Bruce's microtome, I have made a complete series of coronal sections, through two chimpanzee hemispheres and one orang hemisphere, and the evidence afforded by these is precisely the same, although it is not of so striking a character as that obtained from the horizontal sections. The sectional anatomy of the anthropoid cerebrum presents many points of interest in addition to those I have thus briefly touched upon in this paper; but as I hope to deal fully at some future time with this matter, I shall not go further into the subject at present.

Although various observers have made horizontal sections through the cerebral hemispheres of the chimpanzee and orang, chiefly with the view of ascertaining the condition of the posterior horn of the lateral ventricle, I believe that the figures which I publish are the first that represent the arrangement of the caudate, lenticular and thalamic nuclei in the anthropoid ape. Marchand¹ was indeed fully alive to the importance of determining the relation of the lenticular and caudate nuclei to the surface, with the view of throwing more light upon the question of the morphology of the anthropoid insular district. He made a horizontal section through an orang cerebrum, but this was not in a particularly good state of preservation, and he does not figure it. Still, he was led to infer from what he saw that the caudate nucleus extends as far forward as the fronto-orbital sulcus. It may be well to mention that Marchand is a firm believer in the view that the fronto-orbital sulcus in the anthropoids corresponds with the anterior limiting sulcus of Reil in man. Indeed, he and I arrived at this conclusion quite independently of each other, and almost at the same time.

¹ "Die Morphologie des Stirnlappens und der Insel der Anthropomorphen," p. 81.

THE RELATION OF THE FORNIX TO THE MARGIN
OF THE CEREBRAL CORTEX.¹ By G. ELLIOT SMITH,
M.D., Ch.M. (Syd.), *James King Travelling Scholar of the
University of Sydney, St John's College, Cambridge.*

THERE are many points of fundamental importance in the anatomy of the fornix which are almost unintelligible without an accurate knowledge of the morphology of that part of the cortex to which the fornix is so intimately related, and which may be called the 'margin' of the cortex. This region of the brain of man has been recently described in great detail by Gustav Retzius, in a magnificent monograph and atlas (*Das Menschenhirn*, 1896). A long line of investigators, of whom the most recent are Marchand, Paul Martin, and Retzius, have clearly demonstrated the manner in which the margin of the cortex becomes modified during development in certain of the more highly organised mammalia. But the study of the ontogeny of a few of the higher types of brain does not give one an insight into the process of differentiation sufficiently clear to interpret the meaning of the peculiar changes which the margin of the cortex undergoes. Such a knowledge can only be gained by the examination of a large series of brains of widely differing types, provided, of course, that these types can be accurately compared, and the homologies of corresponding parts satisfactorily determined.

This method has been followed in the present communication. The most striking result which proceeds from this line of study is the recognition of the fact that the fornix conforms to one and the same fundamental plan in the arrangement of its fibres in all vertebrates, and even in such dissimilar types as those presented by the Sauropsida and Mammalia.

The best introduction to the study of the fornix is the investigation of the morphology of the margin of the cortex. For, when the modifications which the margin of the cortex

¹ Communicated to the Anatomical Society of Great Britain and Ireland, at Dublin, June 1897.

has undergone in the evolution of the higher type of mammalian brain are understood, it becomes a relatively simple matter not only to trace the fibres of the fornix in their apparently aberrant and devious courses, but also to recognise the significance of these peculiarities.

At the outset it is necessary to explain what is meant by the term 'fornix.' Introduced originally as a purely descriptive term to describe the 'arched' or 'vaulted' (Latin, *fornix*; and German, *Gewölbe*) arrangement of nerve fibres on the ventral aspect of the corpus callosum, the term had no exact meaning to the histologist. With the growth of a more exact knowledge of brain anatomy, various writers have employed the term in very different senses. Thus, while some writers apply it merely to longitudinal uncrossed fibres of one hemisphere, others include crossing or commissural fibres. Others, again, would restrict it merely to the so-called 'anterior pillar' of the fornix and its backward continuation in the hemisphere.

In this communication, the 'fornix' will always be regarded as *all those fibres which arise from or end in the hippocampus, and which, at some part of their course, form constituents of the fimbria or alveus*. This definition will be untenable if, as Koelliker believes, the fornix also derives fibres from the gyrus fornicatus but, upon the morphological grounds advanced in this memoir, the definition just formulated appears to be perfectly justifiable. For this definition includes the whole of a natural group of fibres with a common phylogenetic history, which differs from that of all the other fibre-systems of the cerebral hemisphere.

There are so many elements of confusion in the literature of this subject that it will conduce to clearness and conciseness if the consideration of the various opinions upon this complex region of the brain be deferred until the indubitable facts of the case have been stated.

THE HIPPOCAMPUS IN MAN.

If one examines the mesial surface of a fresh human cerebral hemisphere in which the overhanging folds of the cortex have been gently drawn aside so as to expose the marginal region, he will obtain a view of certain structures which are schematically represented in the first figure.

It is quite unnecessary to enter here into a particular account of all that is shown in this scheme, since its main features are quite familiar to all students of anatomy, and its details will be fully discussed subsequently.

The fascia dentata (*d*) appears as a band of cortex extending from near the temporal pole (*d'*) obliquely upward and backward to the posterior aspect of the splenium (*s*) of the corpus callosum (*c*), where it appears (*d''*) to taper and end. The fimbria (*f*)

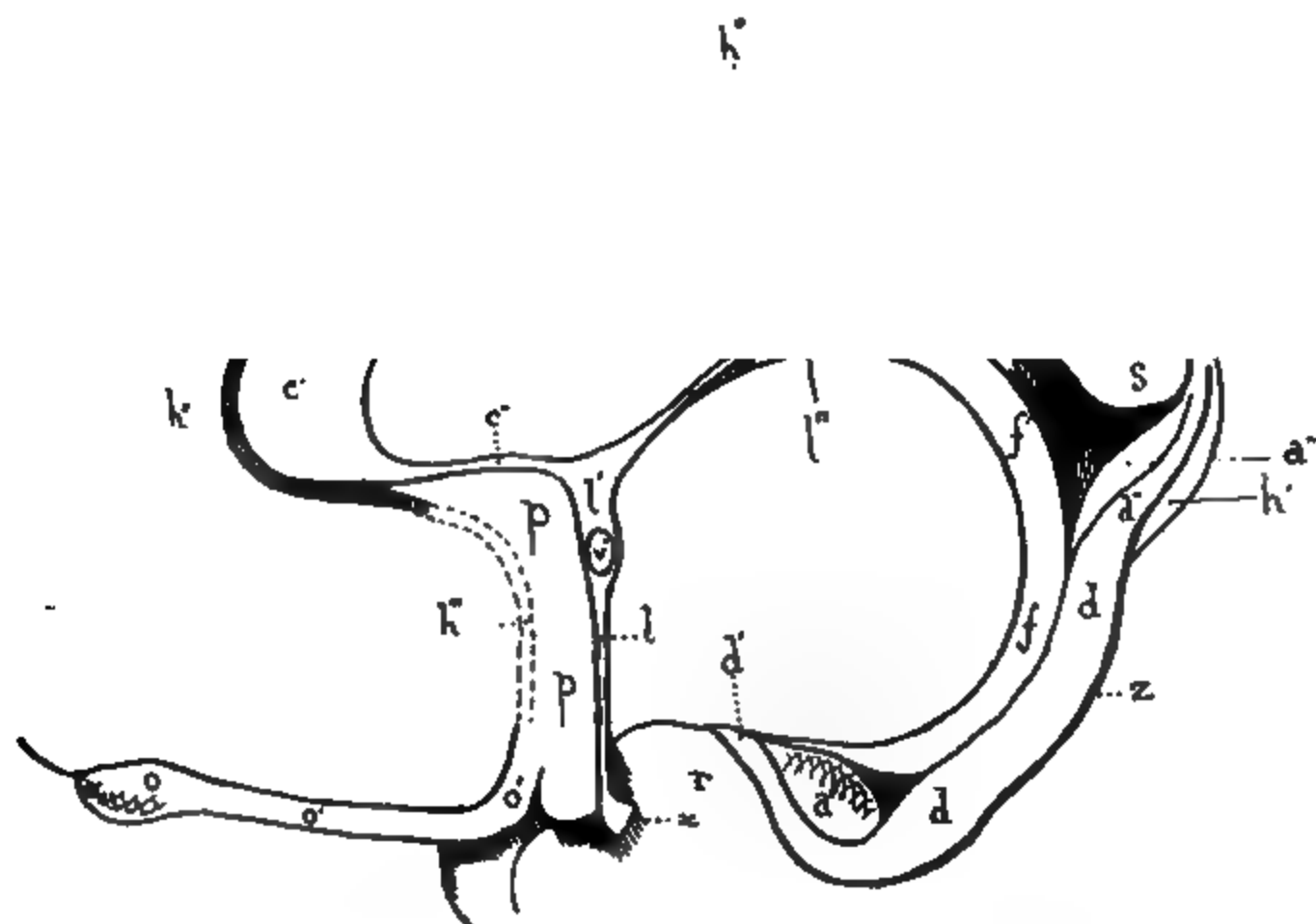


FIG. 1.—Scheme of cerebral commissures, and the margin of the cortex of the human brain.

consists of a white band, placed immediately upon the marginal side of the fascia dentata. It begins in the temporal region, in close proximity to the temporal extremity of the fascia dentata (d'), and accompanies the fascia dentata (except at the point marked a') as far as the inferior aspect of the splenium (s). Here the fascia dentata bends backward (d'') to reach the posterior surface of the splenium (s), but the fimbria continues its upward course in front of the splenium. It thus becomes separated from the fascia dentata by the splenium. After

leaving the fascia dentata this band of fibres is known in human anatomy as the 'posterior pillar' of the fornix (f'). The fimbria (f), and its continuation, the 'posterior pillar,' form a regular curve, which extends right round or, to speak more accurately, forms the margin of the hemisphere. It reaches as far forward as the lamina terminalis (l'), to whose dorsal extremity it presents important relations, which will be subsequently discussed. The anterior continuation of the fimbria and posterior pillar of the fornix is often known, together with its fellow of the opposite hemisphere, as the 'body of the fornix' (f'').

These terms 'posterior pillar' and 'body of the fornix' are mentioned here merely to be discarded. In human anatomy they may be useful and convenient enough, but when they are applied to comparative anatomy they cease to have any value, because they are purely relative and arbitrary terms. In this communication the term 'fimbria' will be understood to include the whole extent of the marginal fringe of medullated nerve fibres ($f.f.f''$) from temporal pole to lamina terminalis (l'), therefore including the 'posterior pillar' and 'body' of the fornix of human anatomy.

These structures—fascia dentata (d) and fimbria (f)—are practically all that can be seen upon the surface of the human brain of that large cortical formation known as the '*hippocampus*,' which forms so prominent a bulging into the lateral ventricle. It is only necessary to glance at a transverse section through the hippocampal formation to appreciate how much of the hippocampus is hidden from view, or submerged below the surface of the hemisphere.

The general and essential features of the hippocampus alter very slightly in the mammalian series, and are so characteristic, when examined histologically, that after appreciating its peculiarities in any given brain, it is quite easy to recognise them in other brains, even when placed among quite different surroundings.

In the brain of the rabbit a form of hippocampus (fig. 2) is found which is typical of the great majority of Meta- and Eutheria, and is therefore better suited for our present purpose than the somewhat special type which the human brain presents.

In this scheme of a section through the hippocampus of a rabbit (*Lepus*), the fimbria (fig. 2, *f*) represents the boundary between the intra-ventricular, epithelium-covered surface (*A*), and the extra-ventricular exposed surface of the region (*a*), because the epithelial choroidal fold which forms part of the ventricular wall is attached to the fimbria. In the figure, *dd* represents the fascia dentata, and *hhh* the rest of the hippocampus. Of the extensive surface area which this hippocampal formation possesses, only a small fragment (*D*)—less than a third—of the fascia dentata appears upon the surface. The rest of the fascia dentata (*d*) and the whole of the surface of the hippocampus proper (*h*) is hidden from view in the depths of the hippo-

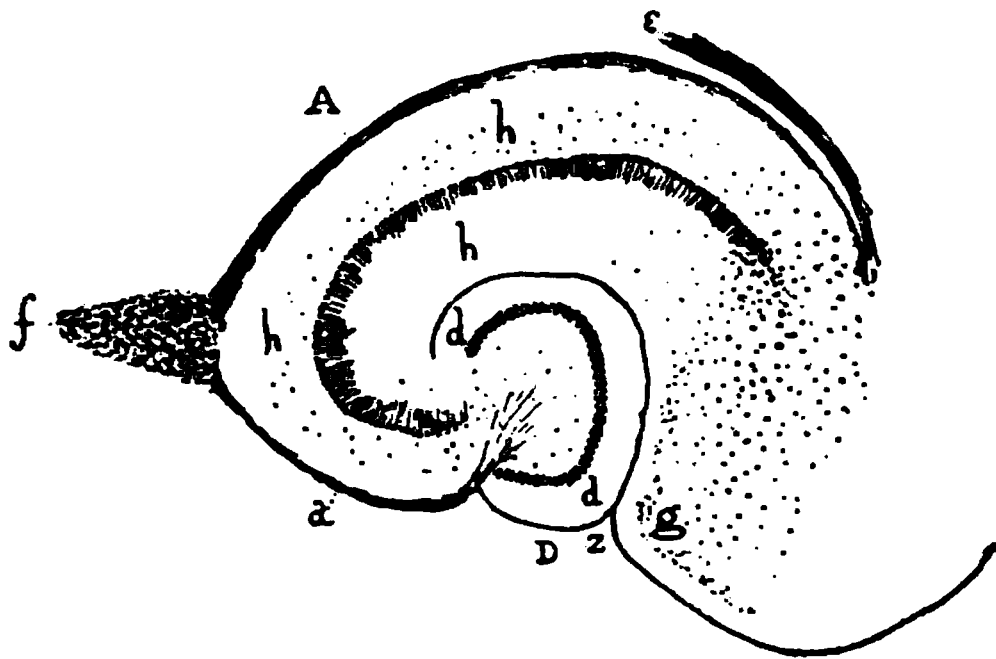


FIG. 2.—Scheme of a section through the hippocampus of a rabbit, at right angles to its long axis. Section stained with *lithium carmine*, and subsequently treated by *Pal's* hæmatoxylin method.

campal fissure, and shut out from participation in the formation of the actual surface of the brain.

But a band of grey substance (*a*), covered with a very thin but definite layer of medullated fibres, is found forming part of the surface between the fascia dentata (*D*) and the fimbria (*f*). This consists of a band of cortex which has become inverted, *i.e.*, its superficial layer is morphologically the 'deep' or ventricular surface, and the medullary covering is the *alveus*, normally the ventricular coat of the hippocampus.

A clearer and more vivid picture of the changes which the hippocampus has undergone in this process of inrolling will be obtained if we imagine the appearance of the hippocampus which has been 'unrolled,' and in which, at the same time, the

fimbria had moved to its primitive position at the exact margin of the cortex, i.e., alongside the fascia dentata. The result of such a simplification is represented schematically in figure 2'. The extent of the real or morphological surface of the hippocampus is thus graphically demonstrated. This figure also shows the original position of that part of the deep surface of the hippocampus (*A'*) which, in the process of inrolling of the hippocampus, becomes pushed beyond the fimbria (*f*), and thus comes to lie upon the surface of the hemisphere outside the ventricle (fig. 2, *a*). This part (*a*) of the hippocampus is obviously inverted.

In figure 2 no part of the morphological surface of the hippocampus proper (fig. 2', *hh*) actually forms part of the surface of the brain. This hippocampal surface is quite hidden

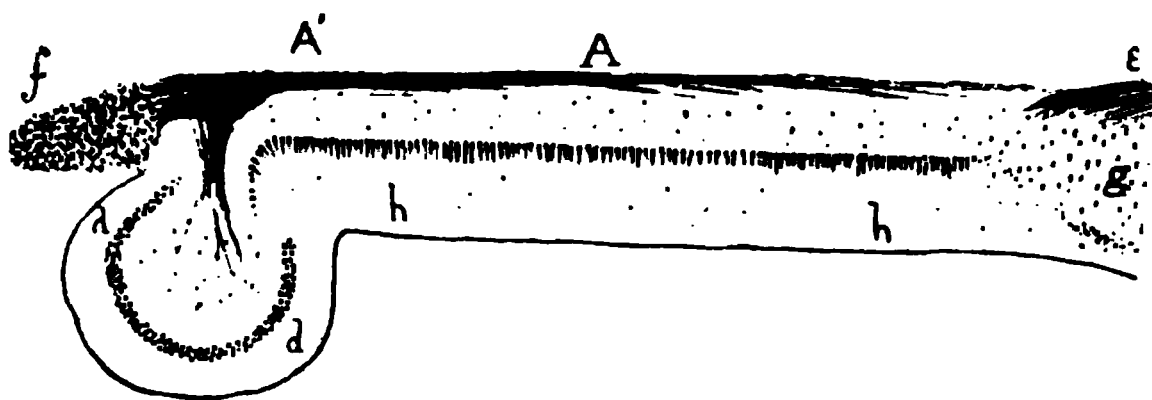


FIG. 2'.—A scheme to represent such a hippocampus as that shown in Fig. 2 after being unrolled, and with the fimbria in its primitive position.

from view in the depths of the hippocampal fissure, and hence may be known as the '*submerged hippocampus*.'

In the brains of most mammals a very definite band of '*inverted hippocampus*,' covered with extra-ventricular alveus, separates the fascia dentata from the fimbria. But in the human brain the fascia dentata (fig. 1, *d*) is in close proximity to the fimbria (*f*) in the greater part of its extent. In fact, if the hippocampus (*hh*) of figure 2' could be imagined wrapped around the fascia dentata (*dd*), so that the pallium (*g*) were in close proximity to the fimbria (*f*), an appearance not unlike that actually found in the brain of man would be the result. But alongside each extremity of the fascia dentata the *inverted hippocampus* becomes apparent. At the temporal end it appears as a large rounded knob (fig. 1, *a'*), which forms the apex of the '*uncus*.' It is covered by only a very thin layer of extra-

ventricular alveus, so that it requires a careful examination to distinguish it from the neighbouring cortical areas. Retzius calls this fragment of inverted cortex the '*gyrus intralimbicus*.' The fascia dentata (*d'*) which separates this boss of inverted cortex from the pyriform lobe (*r*) is very much reduced in size, and has been called '*benderella dell' uncus dell' hippocampo*' by Giacomini (1882). Thus the structure known as 'uncus' in human anatomy consists of three distinct varieties of cortex: (*a'*) inverted hippocampus, which Retzius calls '*gyrus intralimbicus*,' (*d'*) fascia dentata, and (*r*) pyriform lobe. The appearance of a horizontal section through this region is not unlike that represented in figure 2.

In the interval between the upper extremity of the fascia dentata (fig. 1, *d''*) and the splenium (*s*), the inverted hippocampus again makes its appearance (*a''*) as a fusiform band. Retzius also elevates this little fragment of inverted cortex to the dignity of a 'gyrus,' with the distinguishing name '*fasciolaris*.' Zuckerkandl (Ueber d. Riechcentrum, 1887) calls it '*Cauda Cornu Ammonis*,' and Giacomini describes it as the '*Eminenza della fasciola*,' the 'fasciola' being the tapering upper extremity (*d''*) of the fascia dentata. ('Fascia dentata della grande hippocampo,' *Giornali d. Reg. Accad. d. Med. d. Torino*, Nov.-Dec. 1883.)

In man, then, while the margin of the hemisphere is fringed from temporal pole to lamina terminalis by fimbria, the margin of the cortex is fringed with hippocampus in the smaller part of its extent, from the temporal pole to the posterior surface of the splenium. It is therefore evident that the apparent upper extremity of the hippocampus in man (fig. 1, *a'' d''*) is separated from the lamina terminalis (*l'*) by a very considerable interval.

In most mammals the corpus callosum is a very much smaller and shorter structure, both absolutely and relatively, than it is in man; and with this shortening, the splenium is placed relatively much further forward in the hemisphere. In spite of this altered position of the splenium, the apparent upper extremity of the hippocampus in most mammals presents essentially the same relation to the splenium. This implies that the hippocampus fringes the cerebral cortex in a relatively much greater part of its extent in some brains than in others.

In many Eutherian brains the hippocampal arc extends as far forward as the lamina terminalis, so that the grey matter of the hippocampus becomes directly continuous with the grey matter which thickens the dorsal part of the lamina terminalis.

In the cerebrum of a marsupial or monotreme the true corpus callosum is wanting, or, to speak more accurately, the more dorsal of the two cerebral commissures is purely hippocampal. In the hemisphere of such a cerebrum the hippocampal arc extends forward not only as far as the lamina terminalis, but even still further forward.

THE HIPPOCAMPUS IN MARSUPIALS AND MONOTREMES.

The hemisphere of *Phascolarctos*, whose mesial surface has been represented in figure 2 serves as a convenient represen-

the surface present an appearance which closely resembles that of such Eutherian brains as the rabbit, cat, or sheep. Thus three concentric bands are to be found lying in front of the hippocampal fissure—a posterior composed of fascia dentata (d, d'), an anterior of fimbria (f), and an intermediate (a) of *inverted cortex*, covered with extra-ventricular alveus. If a horizontal section, taken at the level of the ventral commissure (v), were examined, an appearance would be presented which might very well be represented by figure 2.

The fimbria (f) sweeps round in a regular curve to the lamina terminalis, just as it does in any other mammalian hemisphere. But the fascia dentata (d) presents a similarly regular curve in the marsupial, and accompanies the fimbria as far forward as that compact band of fibres goes. Arrived at the lamina terminalis, the fimbria ceases to exist as such, and becomes split up into various sets of fibres, of which more will be said subsequently. One of these sets crosses the mesial plane in the thickened upper extremity of the lamina terminalis, and thus contributes to the formation of the dorsal or hippocampal commissure (w).

But the fascia dentata (d) continues its forward course above the dorsal commissure, and, bending downward in front, may readily be traced almost as far as the olfactory peduncle (o').

In discussing the constitution of the hippocampus (*supra*), it was mentioned, as a general law, that wherever the fascia dentata appeared, the rest of the hippocampal formation would certainly be found—it may be *submerged*—at its peripheral border. And the case in point is no exception to the general rule. For, in the depths of the hippocampal fissure, which forms the peripheral limit of the visible part of the fascia dentata, an equally extensive arc of *submerged hippocampus* will be found upon examination.

It may be stated, therefore, that the cerebral cortex of the marsupials is fringed in the whole of its extent from olfactory peduncle (o') in front to the temporal pole behind and below by a typical hippocampal formation.

That portion of the hippocampal arc which is placed behind the region of the lamina terminalis obviously forms the margin of the cerebral cortex, just as the fimbria is the edge of the white matter. The fascia dentata is the real edge of the grey matter

because the more centrally situated *inverted cortex* is morphologically a part of the more peripherally placed hippocampus (*sensu strictu*). In the anterior or precommissural portion of its extent, the hippocampus is not so obviously the margin of the cortex. In fact, anyone who merely examined the surface of the hemisphere would say that the hippocampus is placed between two cortical areas (*y* and *p*). A histological examination shows us that the area *p* corresponds to a ganglionic mass—the *corpus præcommissurale*—which cannot be regarded as cortex in the proper sense, and therefore the hippocampus in this region also forms the margin of the cerebral cortex, and separates the general cortex from what Burdach would call the *Kerngebiete*.

FIG. 4.—Mesial surface of the brain of an *Echidna*, exposed by mesial sagittal section.

In the anterior portion of its extent, the hippocampal arc in the hemisphere of the monotreme presents relations exactly analogous to those just described in the marsupial. The disposition of this region in *Ornithorhynchus* I have already described and figured in this *Journal* (vol. xxx. p. 470). Figure 4 shows the exactly similar general features presented by the brain of *Echidna*. In both monotremes the precommissural part of the hippocampal arc is developed to a much better extent than in any marsupial, so that the distinctive features of the precommissural region stand out with greater prominence in the representatives of this order. A coronal section which passes just in front of the commissures in *Ornithorhynchus*

shows (fig. 5) a very well developed hippocampus (*h*), with a well formed and extensive fascia dentata (*d*). This hippocampus forms a component part of the mesial wall of the hemisphere.



FIG. 5.—Portion of a coronal section of the hemisphere of *Ornithorhynchus*, just in front of the commissures. Stained in same manner as the section represented in Fig. 2.

Its dorsal edge becomes directly continuous with a region which presents all the characters which are recognised as distinctive of typical cortex or pallium (*g*). Thus it presents a graduated series of pyramidal cells of characteristic shape, scattered

throughout the thickness of the wall, the smaller pyramids being, as a general rule, more superficially, the larger more deeply situated; and it possesses a very definite layer of medullated fibres which cover its ventricular aspect (*e*).

The portion of the mesial wall of the ventricle (*p*) which is in direct continuity with the ventral margin of the hippocampus presents features which form a striking contrast to those of a cortical structure. Thus, there is no ventricular covering of medullated fibres. On the contrary, the ventricular surface of the *precommissural body* (*p*) is quite free from nerve fibres, and the only compact collection of nerve fibres in the region is found quite close to the mesial surface. The nerve cells which occur in this mass of grey matter are quite unlike those found in the general cortex, and are not arranged in that definite and characteristic manner which is distinctive of the cortex. On the contrary, stellate and fusiform cells of moderately large dimensions are scattered, apparently indiscriminately, throughout the region, and their axis-cylinder processes, instead of proceeding in the direction of the ventricle, usually pursue a course towards the surface.

The *precommissural body* consists of a thick vertical ganglionic wall, which extends backward on each side from the olfactory peduncle to the lamina terminalis, which links together the two posterior extremities of the precommissural bodies. It presents the same uniform features in all vertebrates, but is relatively much more massive in reptiles, and especially in amphibia. In the developing mammalian brain it presents a similar massive appearance early in development, but becomes thrown into obscurity by the subsequent enormous development of the surrounding cortical structures.

As a matrix for fibres of the fornix, as well as a place of origin of many others, it is of great importance in the study of the fornix system.

THE FORNIX IN ORNITHORHYNCHUS.

In the marsupial and monotreme, the system of fibres connected with the hippocampal arc form a system which remains quite distinct from and unmixed with the fibre systems of the

rest of the cortex. In other words, the series of fibres which spring from the hippocampal arc (fig. 3, *d.d.d*) proceed downward in the concavity of the arc and remain isolated, because the fibres connected with the pallium (*g*) proceed upward, i.e., away from the hippocampal arc. This statement will be more intelligible after studying fig. 5, in which the hippocampal system or *alveus* (*A*) is quite distinct from and unmixed with the general medullary matter or corona radiata (*e*).

It will be evident from the subsequent descriptions that in the Eutherian hemisphere the fornix or hippocampal system becomes intermingled with pallial fibres, and confused in other ways. Hence there is a great advantage in studying this system in the monotreme or marsupial where it is isolated and free from other disturbing elements, which will be discussed subsequently.

It is advisable, in the first place, to gain a clear idea of the fornix in its unmixed and simple condition. Then the influences which modify the hippocampal arc may be discussed, after which it will be a relatively simple matter to appreciate the modifications of the fornix which follow these disturbances.

Behind the region of the lamina terminalis, the fornix (fig. 3, *f*) could not be simpler. All the fibres coming from or going to the extensive post-commissural part of the hippocampal arc are collected into a simple compact strand of fibres—the fimbria (*f*). But in the precommissural region, where all the various constituents of this compact strand become separated one from another, a considerable degree of complexity is introduced. This region is best studied in the monotreme, because the hippocampal or dorsal commissure is a simple bundle, and the anterior part of the hippocampal arc is better developed than in most marsupials. Fig. 6 represents a sagittal section through the commissural and precommissural regions in *Ornithorhynchus*, in which all the constituents of the fornix are extremely clearly demonstrated.

In this figure, *v* represents the ventral commissure, *x* the optic tract, *w* the large group of scattered bundles of the hippocampal commissure, *d* the fascia dentata, *t* the cortex of the *tuberculum olfactorium*, and *p* the precommissural area, which is the surface of the precommissural body. From these landmarks and by

comparison with figs. 3 and 4 (or this *Journal*, vol. xxx. p. 470), it will be easy to locate this section.

The constituents of the fornix in *Ornithorhynchus* may be conveniently divided into a number of groups.

a. Fibres collect from all parts of the hippocampal arc to cross the median plane in the thickened upper extremity of the lamina terminalis. In the Monotremes (fig. 6, *w*) these crossing fibres

x

FIG. 6.—Sagittal section of the commissural and precommissural regions of the hemisphere of *Ornithorhynchus*. Weigert stain. Section passes quite close to the mesial plane.

form a series of scattered bundles, disposed apparently irregularly. In *Phascogaleos* there is very little more attempt at a definite arrangement. But in most Marsupials a definitely crescentic or bilaminar shape is assumed by the dorsal commissure.

β. The *columna fornicis* (*Fasciculus postcommissuralis*).—Fibres (*z*) collect from all parts of the hippocampal arc in the region immediately above the ventral commissure (*v*), and then proceed

backward and downward, closely applied to the ventral commissure. They then enter the thalamic region, and proceed toward the corpus mammillare. Of course, the majority of these fibres come up in the fimbria from the more caudally placed parts of the hippocampal arc. When the commissural fibres enter the lamina terminalis, the fibres of the columna fornicis extend forward in front of them (fig. 6, 2), and hence the latter have often been supposed to be continuations of the former. But a considerable number of fibres belonging to this series arise from the precommissural region of the hippocampus, and as they proceed through the precommissural body (*p*) they curve upwards so as to skirt around the large ventral commissure. These fibres may readily be distinguished in the figure proceeding through the precommissural body in large bundles, which converge above and behind the ventral commissure (2). Here the fibres of the columna (2) appear to intermingle with those of the *stria medullaris thalami* (6) which are ascending to the ganglion habenulæ (*b*). There is here an actual interchange of fibres between the columna fornicis and the stria medullaris (*am*), such as Lotheissen and Koelliker have described in mammals, and Edinger in reptiles.

In *Ornithorhynchus* some fibres of the columna fornicis (2) which spring from the extreme anterior end of the hippocampal arc proceed to their destination below the ventral commissure, instead of above that commissure, like the great bulk of the columna fornicis (2). I have not noticed any fibres which indubitably belong to the columna fornicis following such a course in any other brain.

γ. *The Fasciculus præcommissuralis*.—A large, scattered, and heterogeneous group of uncrossed fibres of the fornix system pursue their course to the base of the hemisphere, or *vice versa*, in front of the ventral commissure, and therefore may well be distinguished as precommissural. The fibres which compose this fasciculus (3) occupy a more superficial position in the precommissural body than any other fibres, and may be distinctly seen crossing over the fibres of the columna fornicis (2). It is the homologue of this precommissural bundle which whitens the greater part of the mesial wall of a bird's cerebral hemisphere, although other more deeply situated fibres, corre-

sponding to the columna fornicis, also contribute in a smaller degree to this result.

The *fasciculus præcommissuralis* undoubtedly contains fibres of very varied significance, and of equally varied destination. But the most obvious constituent is a large series of fibres (3) collected from (or proceeding to) all parts of the hippocampus, which congregate in the precommissural area between the ventral commissure (*v*) and the mesial cortex of the tuberculum olfactorium (*t*), and extend as a compact bundle on to the basal aspect of the brain, immediately in front of the optic chiasma (*x*). In this *Journal* (vol. xxx. p. 480) I have called this bundle the *hippocampo-basal association bundle*. It will be considered subsequently, when the Eutherian fornix is being discussed.

There is a scattered group of fine fibres (4) extending from the precommissural body into the hypothalamus, where they become widely scattered. Their connections are quite unknown. Then there is a third large series of fibres which connect the precommissural body with the deep surface of the cortex of the tuberculum olfactorium (*t*). These fibres (which are not shown in the figure) are probably of great physiological significance as a path for olfactory impulses to the hippocampus.

δ. *Fasciculus marginalis*.—There is yet a fourth set of fibres which enters into the constitution of the fornix. At the ventral margin of the hippocampus, *i.e.*, along the line of junction of precommissural body (*p*) and fascia dentata (*d*), a very distinct bundle of fibres (5) is to be found in *Ornithorhynchus*, *Echidna*, *Macropus*, and probably in all monotremes and marsupials. It can be distinctly traced in front and below to the region of the olfactory peduncle (*o'*), from which it seems to proceed. As it is traced upwards it will be found to give off a regular series of medullated fibres (5'), which extend obliquely upwards and forwards in the molecular or superficial layer of the fascia dentata (*d.d*). When the bundle reaches the region of the lamina terminalis it extends on to the dorsal aspect of the hippocampal commissure, and appears to proceed still further back to more distant parts of the hippocampus. It always presents the same relation to the fascia dentata as it does in the precommissural region (fig. 5). I have on several occasions in

this *Journal* called attention to this important fibre-tract under the name of '*olfactory bundle of the fascia dentata*.' For this cumbersome designation I substitute the more convenient name *fasciculus marginalis*.

THE CHANGES IN THE HIPPOCAMPUS AND FORNIX IN EUTHERIA.

In the Eutherian brain the simplicity and uniformity of the hippocampal arc, and the isolation of the fornix-system springing from it, become disturbed by the invasion of the anterior portion of the hippocampal arc by commissural fibres from the general cortex or pallium which mingle with the commissural fibres of the fornix. In the marsupial, all the commissural fibres of the pallium pass through the ventral commissure, thus leaving the hippocampus and its commissure undisturbed. But in the higher type of mammal, some of the commissural fibres of the pallium cross the median plane along with the hippocampal commissure, and in order to do so they traverse the alveus of the hippocampus. The meaning of this statement will be evident if one were to imagine some of the fibres marked *e* in figure 5 passing along with the fibres *A* instead of in the opposite direction, which they pursue in the figure. This may be expressed in another way by saying that the dorsal commissure extends its area of origin from the hippocampal arc to a neighbouring area of cortex or pallium (*g*) which lies above the anterior part of the hippocampus.

In this way the first confusing element is introduced. The dorsal commissure, instead of being now purely hippocampal, is now a mixture of pallial and hippocampal fibres, the pallial fibres occupying the anterior position, the hippocampal the posterior position in the commissure.

The part of the hippocampus which is invaded by the pallial fibres undergoes a series of degenerative changes, and, as a result, the whole of the hippocampal arc which lies in front of the lamina terminalis becomes reduced to a mere vestige. But, so far, the regular curve of the hippocampal arc has not been disturbed (fig. 7). The hippocampus extends up as far as the lamina terminalis, and is continued forward above the rudimentary corpus callosum as a mere vestige (*h''*), but this vestige at first forms part of the same regular arc as the posterior part

of the hippocampus. This is the state of affairs which exists in certain bats, of which *Nyctophilus* is an example. But the continued crowding into the dorsal commissure of new pallial fibres causes a rapid increase in the size of the 'corpus callosum' as the pallial factor is generally known. This increased size manifests itself mainly in an increased length of the commissure, possibly because such an elongation provides a shorter course for commissural fibres connected with the more anterior and posterior parts of the hemisphere.

The forward extension of the pallial commissure (fig. 7, c) from the dorsal extremity of the lamina terminalis roofs in the postero-superior angle of the precommissural body. In this way a small recess is formed, having lamina terminalis for its

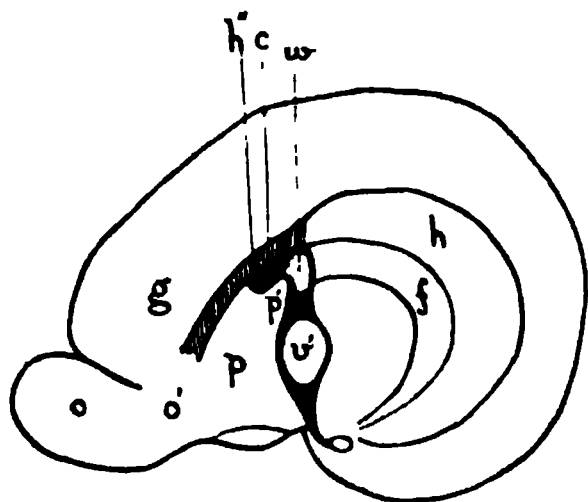


FIG. 7.

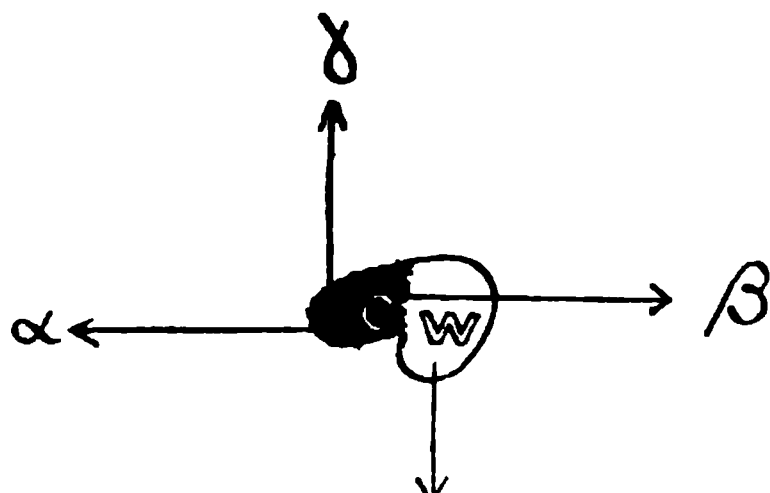


FIG. 8.

FIG. 7.—Scheme to show the relation of a primitive type of corpus callosum to the hippocampus. The degenerated part of the hippocampal arc is shaded (h'').

FIGS. 8, 9, 10, 11, 12, 13.—Schemata explained in text.

posterior wall, the upper part of the two precommissural bodies for its lateral walls, and the corpus callosum for its roof. This recess is the *cavum septi*, and its lateral walls are the *laminae septi pellucidi*.

If the corpus callosum be studied in the course of its development in any of the higher mammals, it will be found to change its position considerably in relation to certain fixed or relatively fixed points. Thus, at its first appearance it is placed immediately upon the dorsal side of the ventral or anterior commissure, and is indistinguishable from the hippocampal commissure with which it is combined. But in the adult, not only has the corpus callosum increased in length, but it has also been raised a considerable distance above the anterior commissure. It may be that the expanding dorsal regions of the pallium

exert some traction upon the commissural fibres which bind them together, and thus tend to raise them also.

Thus we find the pallial element (*c*) in the dorsal commissure exposed to the elongating forces α and β (fig. 8), and to some elevating influence (γ). At the same time, the main bulk of the hippocampal element (*w*) is not only not exposed to such influences but is also possibly held in position by the fimbria (*f*).

The result is, that the corpus callosum becomes elongated and raised (fig. 9), while the main part of the hippocampal commissure (*w*) does not alter its position, although part of it

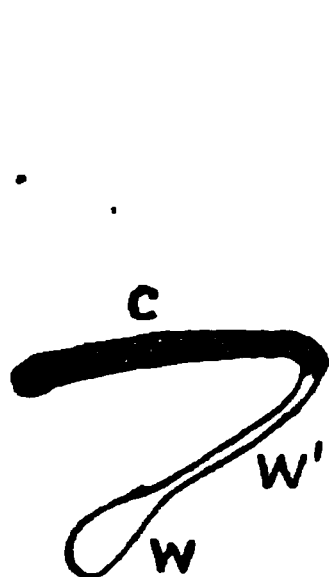


FIG. 9.

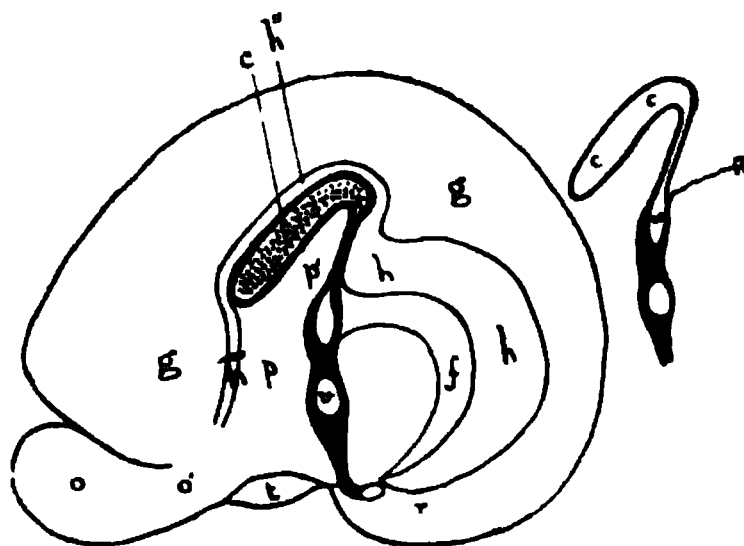


FIG. 10.

FIG. 10.—Schemata to indicate the relation of the corpus callosum to the hippocampus (*h*, *h''*) and the effect produced by the former as it grows above the roof of the forebrain (*R*) in indenting the hippocampal arc and stretching the precommissural body (*p*, *p'*).

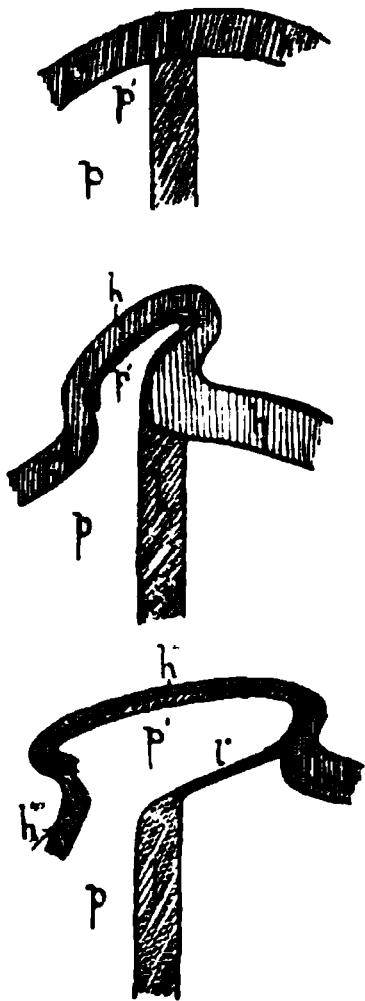
becomes extended and drawn up (*w'*) by the growing corpus callosum.

In its backward growth the corpus callosum meets with an obstruction in the shape of the undegenerated part of the hippocampal arc, which reaches as far forward as the lamina terminalis (fig. 7, *h*). To overcome this obstacle the growing commissure extends obliquely upward and backward above the undegenerated part of the hippocampus (fig. 10, *h*). In doing so, it stretches and carries with it the vestigial remains of the hippocampus (*h''*) which clothe its dorsal surface. The postero-superior part of the precommissural body (*p'*), which has become roofed by the corpus callosum, and which fills up the interval between the latter and the hippocampal commissure (*w w'*), now forms a leaf of the septum pellucidum, and has also been carried

back by the growing commissure to occupy a position upon the dorsal side of the undegenerated part of the hippocampus.¹

Since the corpus callosum develops and extends *within* the concavity of the hippocampal arc, it must profoundly affect the arrangement of this arc, and disturb its relations to the pre-commissural body and lamina terminalis.

According to the relation of the hippocampus to the lamina terminalis, all mammals and vertebrates possessing a hippocampus may be shown to conform to one of three types, which are systematically demonstrated in the figures 11, 12, and 13.



FIGS. 11, 12, 13.—Three schemata to show the varying relation of the hippocampus (*h*, *h''*, *h'''*) to the lamina terminalis (*l*, *l''*) and pre-commissural body (*p*, *p'*) in different groups of mammals.

First type (fig. 11).—The hippocampus (*h*, *h''*, *h'''*) extends forward in each hemisphere above and beyond the thickened lamina terminalis (*l*), and the grey matter of the two structures become continuous. Found in certain cheiroptera, all marsupials, monotremes, sauropsida, and amphibia.

Second type (fig. 12).—The hippocampal arc (*h*) extends to the lamina terminalis (*l*), but in front of this point it is degenerated. Its precommissural part (*h'''*) retains its primitive relation to the precommissural body unchanged. But the intermediate part of the hippocampal arc (*h''*) has been pushed upwards by the corpus callosum, and, since its two ends are fixed, it has become stretched and indented to a varying extent.

This type is found in a large number of mammals, of which the rabbit and hedgehog are examples.

Third type (fig. 13).—This type differs from the second merely in the fact that the larger corpus callosum has carried back the 'hippocampal flexure' (*h*), so that the undegenerated

¹ In a recent memoir I have discussed certain aspects of this question more fully ("The Origin of the Corpus Callosum: a comparative study of the Hippocampal Region of the Cerebrum of Marsupialia and certain Cheiroptera," *Transactions of the Linnean Society of London*, vol. vii. pt. 3, 2nd series, 'Zoology,' pp. 47-69, plates 15 and 16, June 1897).

hippocampus does not reach as far forward as the lamina terminalis (*l'*). But a derivative of the lamina terminalis has been carried backward (*l''*) to form the floor of the cavum septi. This lamina (*l''*) also serves as a matrix for scattered fibres of the hippocampal commissure, under the names *psalterium* and *lyra*. This arrangement of the hippocampal commissure in a broad lamina is well known,—*e.g.*, in the human brain.

This type is found in the more highly developed mammalian brains.

The distinction between the first (fig. 14) and second (fig. 15)



FIG. 14.—Coronal section of cerebrum of *Perameles*, passing through the two cerebral commissures.

types will be rendered clearer by the examination of coronal sections.

A coronal section passing through the two cerebral commissures of *Perameles* (fig. 4) shows the typical arrangement of the commissures, and their relations to surrounding parts in a Marsupial. Both commissures—ventral (*v*) and dorsal (*w*)—are contained in the thickened lamina terminalis, a thin film (*i*) of which is often visible upon the upper surface of the dorsal or hippocampal commissure. This film (*i*) of grey matter I have distinguished by the name *indusium verum* (*Anatomischer Anzeiger*, Bd. xiii. p. 24). Upon each side the hippocampus (*h*) rests upon its commissure; and it is obvious that the matrix of this commissure, which consists of the thickened lamina terminalis, must be in direct continuity with the hippocampus in each hemisphere. This is the reason why the hippocampus has been

represented in fig. 11 (*h''*) *resting upon* the thickened lamina terminalis (*l*).

Fig. 15 represents a scheme of a corresponding section through a brain of the second type (fig. 12), and fig. 16 is a scheme to indicate the plane in which the section has been made. The main mass of the hippocampal commissure (*w*) occupies the same position as in the Marsupial (fig. 14). The hippocampus (*h*) is placed upon the dorsal aspect of its commissure, just as it is in the Marsupial, but it presents a different appearance, because the section passes through the *hippocampal flexure*,—i.e., through the hippocampus where it is bending back to join the vestigial hippocampus which covers the corpus callosum (*c*).



FIG. 15.

FIG. 16.

FIG. 15.—Scheme of a section through the corresponding region of a Eutherian brain.

FIG. 16.—Explains the plane of the section shown in Fig. 15.

The corpus callosum (*c*) is situated in this section upon the dorsal aspect of the hippocampus, and carries upon its dorsal surface the vestigial remains of part of the hippocampal arc (*h''*).

The general nature of the disturbing influence of the corpus callosum, and the manner in which it affects the hippocampal arc, has now been briefly reviewed.

A brief description of certain specific examples of widely different Eutherian brains will help to complete the picture of the evolution of the hippocampal arc, and will, at the same time, show the effect of this evolution upon the fornix.

The hedgehog (*Erinaceus*) affords a very instructive example

of the second type of brain to which reference has been made above. It possesses a small, very obliquely placed corpus callosum (figs. 17 and 18), which has produced a minimal amount of disturbance of the hippocampal arc. In fig. 18 the position which the anterior part of the hippocampal arc would occupy in a marsupial brain is indicated by dotted lines (h''). By comparing this original position of the arc with its vestiges (h'), it is evident that only a small segment of the arc has degenerated, and been pushed upward by the corpus callosum.

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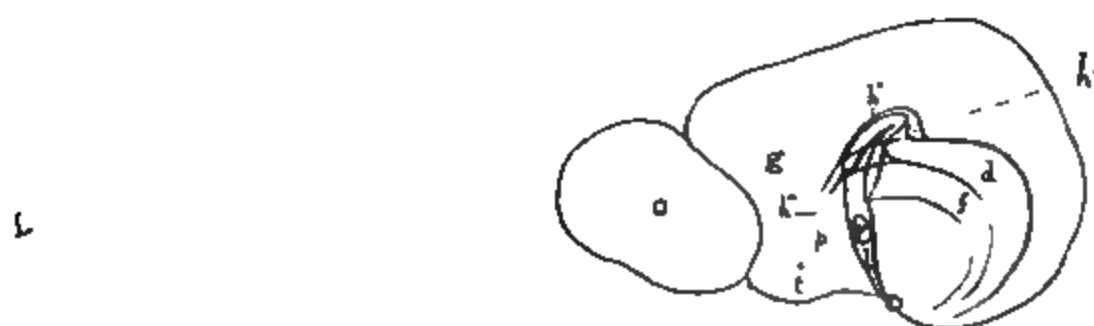


FIG. 18.

FIG. 17.

FIG. 17.—Sagittal section through commissures and neighbouring structures in *Erinaceus*. Weigert stain.

FIG. 18.—Medial surface—hemisphere of *Erinaceus*.

The main mass of the hippocampal or fornix commissure (fig. 17, w) retains its original position unchanged, but a fairly strong bridge of transversely cut commissural fibres (w') still connect it with the splenium (s) of the corpus callosum (c).

If the fascia dentata (fig. 18, d) be traced forward, it will be found to extend right up to the posterior surface of this wall of commissural fibres (w'), and then take a sudden bend upward and backward towards the splenium. This is the *subsplenial hippocampal flexure*. A relatively large representative of the

vestigial hippocampus may be traced along the dorsal aspect of the corpus callosum (h''). But it does not stop there, but is continued forward along the line of separation of pallium and precommissural body (h'''), *i.e.*, in the position where the precommissural hippocampus is found in marsupials and monotremes.

In the marsupial, the *indusium verum* (fig. 14, *i*) has already been noted, joining the hippocampus on the two sides of the middle line. Similarly, in the brain with a corpus callosum (fig. 15) the rudimentary hippocampi (h'') on either side of the mesial plane are joined by a similar true indusium. The term *indusium griseum* is generally employed to indicate the grey film composed of these three structures—the two rudimentary

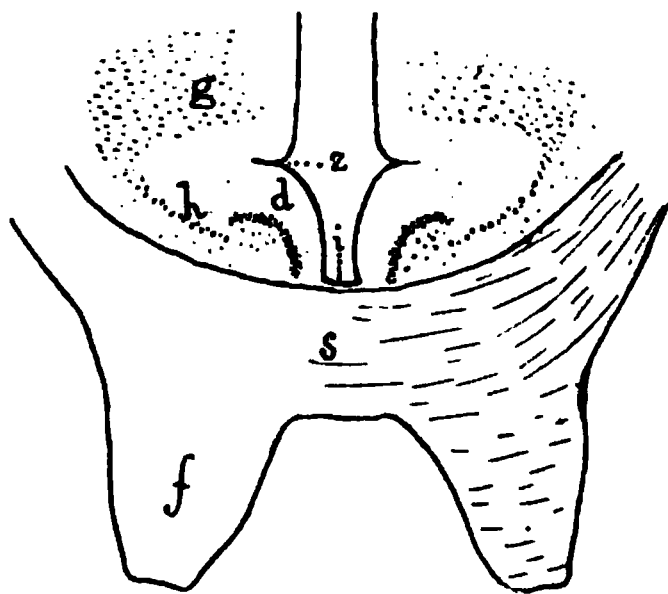


FIG. 19.—Coronal section through splenium and neighbouring structures.
Nyctophilus. Carmine stain.

hippocampi and the mesial grey film. I have introduced the term *indusium verum* to distinguish this mesial bond from the hippocampus or 'false indusium.'

The relation of these structures is extremely well shown in a coronal section (fig. 19) through the splenium (*s*) of the dorsal commissure of a small bat (*Nyctophilus Timoriensis*). A small, somewhat flattened, but otherwise perfectly developed hippocampus (*h*), with a well-formed if simple fascia dentata (*d*), is found resting upon the upper surface of the dorsal commissure on either side of the median plane. These two hippocampal formations are connected with one another by a thin film of grey matter—the *indusium verum* (*i*).

If one were to imagine a hippocampus like that shown in

fig. 19, but in which the fascia dentata had become reduced to very insignificant proportions, or had entirely vanished, he would have an accurate picture of the state of the vestige of the hippocampus which is found resting upon the dorsum of the corpus callosum of the hedgehog. But the pyramidal cells of the hippocampus which remain in this vestigial hippocampus,



FIG. 20.—A cell from the vestigial precommissural hippocampus of *Erinaceus*.
Golgi stain.

both in supra- and pre-commissural regions, are well-formed cells, presenting the characteristic appearance of pyramidal cells of the hippocampus. One of these cells, which is drawn from a coronal section through the precommissural hippocampal rudiment in *Erinaceus*, which had been stained according to the method of Golgi, is figured here (fig. 20). It is a typical

example of a 'double-pyramid,' as Koelliker calls cells which possess a large basal bunch of processes (*B*) in addition to the long apical processes which extend toward the surface.

In the neighbourhood of the splenium, where the complicated and fully formed hippocampus gives place to the simple flattened supracommissural band (without any fascia dentata), which represents the anterior part of the hippocampal arc, some interesting transitional features make their appearance. In all mammals which possess a well-developed corpus callosum, a small projection of cortex invariably crops out behind the fascia dentata, in close proximity to the splenium. It is visible in figs. 17 and 18 (*h'*). Since Anders Retzius called attention to it in 1856, quite a literature of its own has gathered around this unimportant and insignificant little body. Zuckerkandl (who called it the *Balkenwindung*), Gustav Retzius, Rogner, and Giacomini have contributed most to the description of this structure, and have advanced very varied theories to explain it.¹ The homology of this so-called *Balkenwindung* or *Gyrus Andreae Retzii*, as Gustav Retzius calls it, is quite clear, and the meaning of its projection in the splenial region is also easily explicable.

A glance at fig. 21, which represents a sagittal section through the splenium and subsplenial hippocampal flexure of the rabbit, shows the nature of this much disputed little cortical area. The region marked *h'* is the '*Balkenwindung*,' and it is nothing else (at any rate in the rabbit) than that part of the hippocampus which elsewhere is *submerged* coming to light again. When discussing the '*submerged hippocampus*' it was remarked that writers were often inclined to forget the existence of this part of the hippocampus, simply because it is hidden. This is a case in point. For, now the '*submerged hippocampus*' does crop out, there is a very prolonged discussion as to the nature of the strange body. Of course, when this outcrop of the true hippocampus (*h''*) is traced in the caudal direction, it becomes continuous with the general cortex (*g*) of the gyrus fornicatus. In comparing the so-called '*Balkenwindungen*'

¹ Space forbids the discussion of these varied views in this place. Statements of them will be found in full in the recent monograph of Gustav Retzius (*Das Menschenhirn*, 1896) and in the laborious memoir of Giacomini (*Fascia dentata del grande hippocampo*), *Giorn. d. Reg. Accad. di Med. di Torino*, 1883).

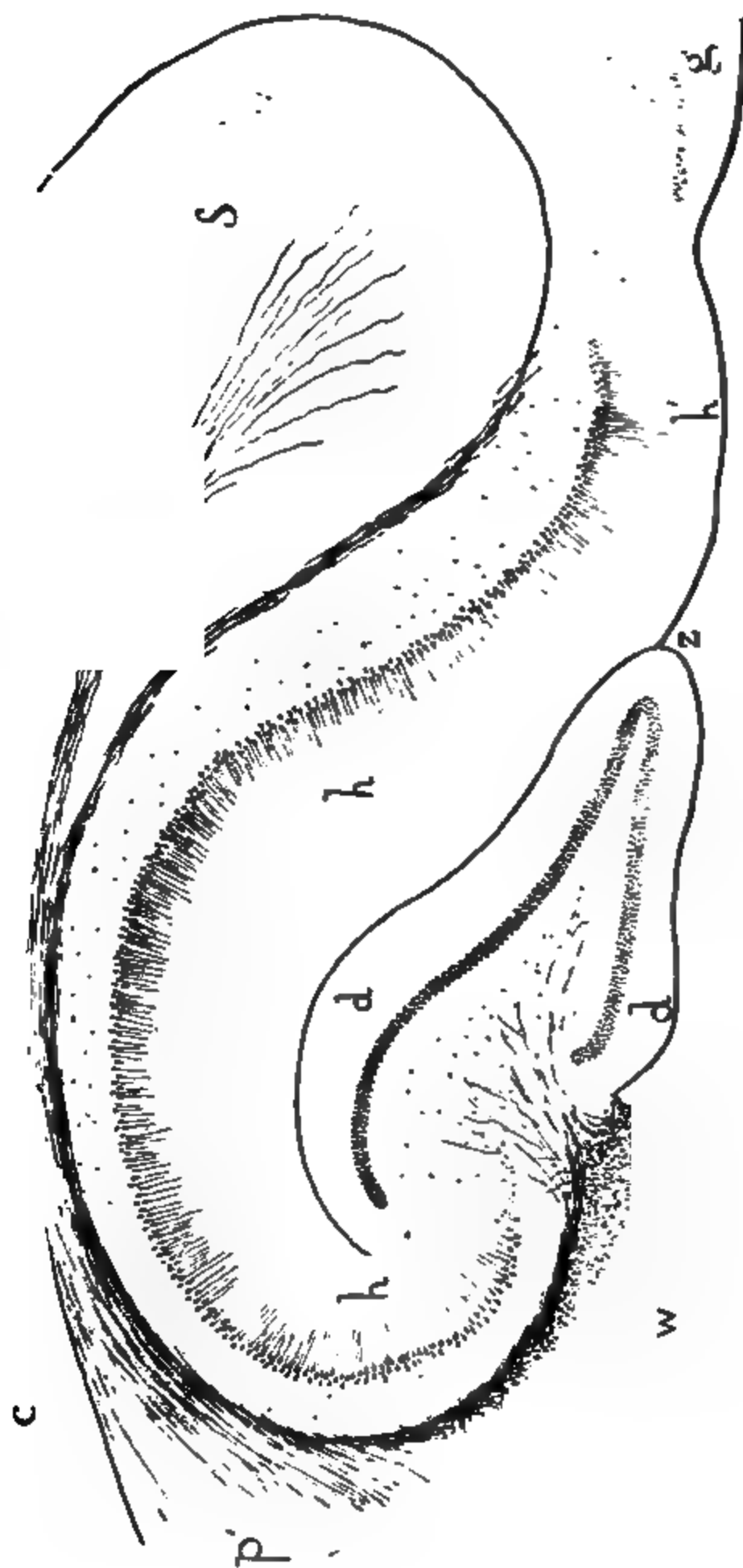


FIG. 21.—Sagittal section through the subcallosal hippocampal flexure, close to mesial plane—rabbit. Stained as in Fig. 2

of different animals, writers often include a mixture of hippocampal cortex (*h''*) and gyrus fornicatus (*g*) of one animal to compare with a knob of pure hippocampus of another. There can be no question of the correctness of the view of Giacomini that

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FIG. 22. —Portion of mesial surface—brain of cat.

it is a '*dipendenza del corno di Ammone*.' Why does it crop out in this situation, and nowhere else? This little piece of exposed hippocampal surface is always found in the region of the splenium, where the complexly inrolled hippocampus is becoming transformed into a simple flattened band,—is, in fact,

becoming unrolled. The inrolling of the hippocampus, and therefore the hiding of the 'submerged hippocampus,' is very closely related to the development of the fascia dentata. It is quite conceivable that the rapid diminution of the dimensions of the fascia dentata, as it proceeds around the splenium, may be a factor in the process of unrolling. One is not inclined to attach much importance to any mechanical effect the backward growth of the corpus callosum might have in this process.

In the cat (fig. 22) the corpus callosum has attained considerably larger dimensions than in the hedgehog, and has carried back the upper extremity of the undegenerated hippocampus away from the lamina terminalis. Thus, it conforms to the third type (*supra*). The brain of the cat affords an excellent



FIG. 23.—Sagittal section of commissures and fornix of *Midas*. Weigert stain.

example of the manner in which the fascia dentata (*d''*) tapers as it proceeds backward from the hippocampal flexure upon the under surface of splenium (*s*). In front of the fascia dentata there is a narrow strip of *inverted cortex* (*a''*), similar to that which occurs in the analogous situation in the human brain. The vestigial hippocampus (*h''*), after extending over the whole length of the corpus callosum, appears in front of the genu (*c*). The dotted line (*h'''*) represents approximately the situation of the precommissural vestige, *i.e.*, the line of separation of the precommissural body (*p*) from the pallium (*g*).

The two parts (*p* and *p'*) of the precommissural body are now very well shown. The dorsal part is the septum pellucidum (*p'*). The ventral (*p*) corresponds roughly, but not exactly, to the *gyrus subcallosus* of Zuckerkandl.

The marmoset *Midas* provides an example of an extreme type of development of the corpus callosum in a brain sufficiently small for accurate histological study. The relatively enormous corpus callosum (fig. 23, *c' c s*) is still placed somewhat obliquely. The hippocampal commissure (*w*) still retains its original place, but is now reduced to very small proportions. But no trace can be discovered of any bridge of commissural fibres between the hippocampal commissure (*w*) and the splenium (*s*) of the corpus callosum. Now that the hippocampal commissure is reduced to such small proportions, its matrix (indicated in outline) of grey matter is very evident, and to it the roof of the forebrain (*R*) is attached. Beever failed to find any hippocampal commissure in *Hapale*, but the explanation of this fact is probably because he looked for it in the region of the splenium (*Philosophical Transactions*, 1891).

THE FORNIX OF EUTHERIA.

The manner in which the fornix is disposed in the hemisphere of one of the higher mammals will be more intelligible now that the plan of the hippocampus is known.

Two things must be constantly borne in mind in this connection,—(1) that the anterior part of the hippocampal arc is degenerate and dislocated; and (2) that the dislocating factor the corpus callosum, has made its appearance within the hippocampal arc, and in the very midst of the fibres of the fornix which are collecting there (compare figs. 6 and 17).

a. Commissural fibres of the fornix.—The disposition of the commissural fibres of the fornix has already been incidentally described in discussing the commissures.

β. Columna fornicis.—The fibres of the columna fornicis arise, in all probability, as axis-cylinder processes of the pyramidal cells [*double-pyramids*] in all parts of the hippocampal arc, both undegenerated and vestigial. The vast majority of its fibres naturally arise from the extensive undegenerated posterior part of the arc, and are brought up to the septum pellucidum in the fimbria. After the commissural fibres from the fimbria have bent in a mesial direction to cross the middle line in the lamina terminalis (figs. 17 and 23, *w*), the non-crossing fibres continue their forward course in the precommissural body. In this way

they appear, in sagittal section, to spring from or pass between the fibres of the hippocampal commissure (fig. 17).

In addition to the fibres which spring from the posterior part of the hippocampal arc, other fibres of the columna fornicis (fig. 17, 2) take their origin from the hippocampal flexure as well as from the vestigial remains which surround the corpus callosum (h''), and are placed in front of it (h'''). The origin of these fibres (which are well known as the *stria alba Lancisii*) from cells in the so-called *indusium griseum* has been described in the rabbit and mouse by S. Ramón y Cajal (*La Cellule*, tome 7). They may also be demonstrated in the hedgehog, springing from the cells of the precommissural vestige of the hippocampus (h'''). To reach the precommissural body or septum pellucidum some of these fibres perforate (*i.e.*, pass between the fibres of) the corpus callosum, others extend around the genu of the corpus callosum (fig. 23, *L*). When they reach the precommissural body all the fibres of this columna fornicis (2) behave just as they do in *Ornithorhynchus* (fig. 6).

γ. *Fasciculus præcommissuralis*.—If the *precommissural bundle* (fig. 17, 3) be traced upward, the great majority of its fibres will be found to bend backward, and *appear* to enter the hippocampal commissure. In reality, they enter the fimbria, just like the fibres of the columna fornicis, and are there indistinguishable from the other constituents of the fimbria. A very distinct group of these precommissural fibres may be traced upward, to pass around the genu of the corpus callosum and enter the so-called *stria alba Lancisii* (figs. 17 and 23, *L*). Others, again, perforate the corpus callosum, to reach the supracommissural vestige of the hippocampus. These fibres of the columna fornicis and *fasciculus præcommissuralis* are called *fibræ perforantes* by Koelliker, who believes that they proceed from the gyrus fornicatus.

If the fibres of the precommissural bundle be traced in the ventral direction, they will be found to behave just like their homologues in *Ornithorhynchus* (fig. 6).

The great majority of them (corresponding to the *hippocampobasal association bundle* of *Ornithorhynchus*) extend on to the ventral aspect of the brain, immediately in front of the optic tract. Here they may be traced for a variable distance in

the lateral direction before they disappear. For convenience of description, this may be called the tract *a*.

A small hypothalamic bundle of fibres (figs. 6 and 23, 4) is present in all the brains which I have examined. This may be called the tract *b*. In all brains there is an intimate connection between the medullary matter of the cortex of the tuberculum olfactorium (*t*) and the fibres of the precommissural body (*p*), which Ganser long ago described in the mole. These fibres are included in the bundles shown in figs. 14 and 15 (*f.p*). This may be called the tract *c*.

The *fasciculus præcommissuralis* is often called the *pedunculus septi pellucidi*, because most of its fibres appear to come from the septum pellucidum. It is also equally well known as the *pedunculus corporis callosi*, because it derives a bundle of fibres from the stria Lancisii (*L*), which appear to the naked eye to come from the corpus callosum itself. The part of bundle *a* which is visible upon the base of the brain has been called the *bandelette diagonale* by Broca.

Koelliker, following Zuckerkandl, calls the precommissural bundle the *Riechstrahlung des Septum*, and says that it ends in the *ganglion basale* of Ganser. This ganglion is a mass of grey matter lying between the optic chiasma and the cortex of the tuberculum olfactorium. He also describes a second or anterior series of septal fibres, which he homologises with the peduncle of the septum pellucidum and peduncle of the corpus callosum. He says that these terminate in the gyrus fornicatus (in the cat), immediately in front of the tuberculum olfactorium ("Ueber der Fornix longus," &c. &c., Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich, xli., 1896, Jubelband, p. 555).

In the rabbit, Koelliker (*loc. cit.*, p. 550) describes the ending of the so-called '*Riechstrahlung*' in the ganglion basale (corresponding to tract *a* of this paper), and in the cortex of the tuberculum olfactorium (tract *c*).

A very great variety will be found in the descriptions which have been given of the fibre-tracts of this region within recent years.

But the following facts can be readily and certainly determined.

In all animals there is a very large series of fibres which pursue a vertical course in front of the anterior commissure. They are connected with all parts of the hippocampus, with its undegenerated and rudimentary portions. Many of these fibres arise in the precommissural body (gyrus subcallosus and septum pellucidum) from the multipolar nerve cells there. Below they extend on to the basal surface of the brain, where many of them can be traced as far as the region surrounding the nucleus amgydalæ.

There is no justification for the name '*Tractus septo-mesencephalicus*' which Edinger gives to this series of fibres in reptiles. (In mammals he calls its homologue the *tractus olfactorius septi*,—i.e., he confuses tracts *a* and *c*.)

By 'mesencephalic tract' he apparently refers to the tract *b*, which I have spoken of as the hypothalamic tract.

The existence of the *fasciculus marginalis* (fig. 6, 5) in higher mammals has not yet been certainly established. In his description of the nerve fibres found in the molecular layer of the fascia dentata in such small mammals as mice, Ramón y Cajal mentions "fibras nerviosas collaterales y terminales de la sustancia blanca del álveo." ("Estructura del asta de ammon," *Annales de historia natural*, xxii.) It seems not unlikely that these fibres may be the terminations of the *fasciculus marginalis*. The marginal bundle (fig. 6, 5) pursues its backward course upon the dorsal aspect of the hippocampal commissure, and above the position where the corpus callosum develops. Its position corresponds, therefore, to that occupied by the *stria mesialis Lancisii* in the Eutherian brain. It is not improbable that its homologue will be found as a constituent of this stria. In the cat, Koelliker figures certain fibres (*loc. cit.*, p. 554) which he calls 'pedunculus corporis callosi' (*Pcc*). He describes the course of this bundle from the stria mesialis around the genu of the corpus callosum, to terminate in the ventral part of the gyrus fornicatus, immediately in front of the tuberculum olfactorium. This so-called part of the 'gyrus fornicatus' appears to be the insertion of the olfactory peduncle (fig. 22, *o'*) into the hemisphere. The so-called 'pedunculus corporis callosi' also seems to correspond to the *fasciculus marginalis*.

THE MARGINAL CORTEX.

Within recent years many investigators have endeavoured to justify the crude scheme of a limbic or falciform lobe, which Broca first definitely enunciated ; and they have also applied the idea of complete cortical arcs to various structures which are placed concentrically within this so-called limbic lobe.

Thus Zuckerkandl described a *Randwindung* or marginal gyrus which consists of two large arcs—outer and inner.

He included in the *outer arc* the fascia dentata, the vestigial hippocampus (which he called ‘gyrus supracallosus’ and ‘gyrus geniculi’), and believed that this arc was continued into the inner root of the olfactory apparatus.

His *inner arc* was composed of fimbria, lamina septi pellucidi and the basal part of the precommissural body (which he called *gyrus subcallosus*).

A glance at fig. 1 shows how illogical this division is. For while he includes the fascia dentata, he apparently excludes the *submerged hippocampus*. Yet he includes his *gyri supracallosus et geniculi*, which merely represent the anterior continuations of the *submerged hippocampus*. Then, again, what advantage is gained by grouping a band of white fibres—the fimbria—with a ganglionic mass—the precommissural body (lamina septi pellucidi and gyrus subcallosus), and calling the result the inner bordering ‘gyrus.’

Retzius, in his recent monograph, adopts a very similar classification, mainly upon developmental grounds.

He includes in the outer ‘*Randbogen*’ the fascia dentata, corpus callosum, fasciola cinerea, ‘*Balkenwindung*,’ stria Lancisii and tænia tecta, gyrus geniculi and gyrus subcallosus. His inner ‘*Randbogen*’ includes the fimbria and septum pellucidum.

The same remarks apply to this division as have been applied to Zuckerkandl’s, but there are here some more extraordinary combinations. Like Zuckerkandl, he ignores the ‘submerged hippocampus,’ yet he includes part of the same formation—the ‘*Balkenwindung*’—apparently because it can be seen. He includes one part of the *precommissural body*—the gyrus subcallosus—in the *outer* and the rest of the same body (septum pellucidum) in the *inner arc*.

This year in his *Traité d'Anatomie humaine* (1897), Testut makes the following remarkable statement on page 294:—"Je considère le corps godronné [fascia dentata], les tractus de Lancisi, les péduncules du corps calleux et la bandelette diagonale comme constituant une seule et même formation—une circonvolution rudimentaire inclusé dans la grande circonvolution limitée par Broca." Being interpreted, this statement simply amounts to this: Testut regards the fascia dentata [the highly specialised marginal region of the hippocampus], the stria Lancisii [the degenerated forward continuation of the hippocampus of which the fascia dentata has practically disappeared], the peduncles of the corpus callosum [part of the precommissural body], and the diagonal band of Broca [the substantia cinerea of Stielia] as a single rudimentary 'convolution.'

It has become very difficult within recent years to know what authors understand by the term 'convolution' or 'gyrus.' Thus Retzius, in his recent work, applies the term 'gyrus' to any little area of the surface of the hemisphere—either grey or white matter—which either is or appears to be of a different nature from neighbouring structures. But Testut, in the instance under consideration, goes to the other extreme, and includes under the term 'circonvolution' a strange and heterogeneous assortment of surface areas.

The scheme of the human brain in the first figure sufficiently explains the views of the present writer as to the nature of the margin of the cortex.

EXPLANATION OF REFERENCE LETTERS.

A, *alveus*.

a,)
a',) *extraventricular alveus*.
a'',)

b, *ganglion habenulae*.

c, *corpus callosum*.

c', *genu*.

¹ In this contribution the terms '*stria Lancisii*,' '*peduncles of the corpus callosum*,' and '*diagonal band of Broca*' have been applied to fibres only, but Testut evidently refers to the grey matter in which these fibres are situated.

c.s., *corpus striatum*.

$\left. \begin{array}{l} d, \\ d', \\ d'', \\ D, \end{array} \right\} \textit{fascia dentata}.$

e., *corona radiata*.

$\left. \begin{array}{l} f, \\ f', \\ f'', \end{array} \right\} \textit{fimbria}.$

g., *general cortex or pallium*.

$\left. \begin{array}{l} h, \\ h', \\ h'', \\ h''', \end{array} \right\} \textit{hippocampus (distinct from fascia dentata)}$

i., *indusium verum*.

k., *commissura mollis*.

$\left. \begin{array}{l} l, \\ l', \\ l'', \end{array} \right\} \textit{lamina terminalis}.$

m., *corpus mamillare*.

n., *pyramidal cells of hippocampus*.

o., *olfactory bulb*.

o', *olfactory peduncle*.

p., *corpus præcommissurale*.

(*p.*, *gyrus subcallosus*.)

(*p'*, *septum pellucidum*.)

r., *pyriform lobe*.

R., *roof of forebrain*.

s., *splenium corpus callosi*.

t., *tuberculum olfactorium*.

v., *ventral commissure*.

v', *anterior commissure*.

$\left. \begin{array}{l} w, \\ w', \end{array} \right\} \textit{hippocampal commissure}.$

x., *optic chiasma*.

z., *hippocampal fissure*.

SOME OBSERVATIONS ON THE STRUCTURE OF THE
RECTUM. By WALTER J. OTIS, M.D., Boston, U.S.A.

THE first important description of the permanent transverse folds occurring on the inner surface of the rectum was given by Houston in the Dublin Hospital Reports for the year 1836. In this description Houston regarded these folds as a part of the normal structure of the rectum serving the purpose of valves to hold back the contents of the rectum during the interval between defecation; and ever since, they have been referred to by English, French, and American writers, as Houston's valves of the rectum. The number of valves that Houston described was four, situated in the lower portion of the rectum alternately, at varying intervals. On the cadaver, or living subject, the lower valves can be easily examined with the finger *per anum*, after having first distended the rectum with air or water. They can also be readily seen by placing the subject for examination in the knee-chest position, and looking up through the distended anus. A striking feature in the distended rectum, other than the amount of distension of which it is capable, is the fact that its internal surface is not tubular in character, but is divided off into large rounded sacculations, separated from each other by large transverse folds of mucous membrane—the valves of Houston. These folds are semilunar in shape, with their deepest portions on the sides of the rectum, and they are arranged in alternate succession at varying intervals. The number that can be seen in this way is generally two or three, but by pressing aside the uppermost fold, another higher up can often be brought into view. The *sphincter ani tertius* of Hyrtl and the *sphincter supérieur* of Nelaton were undoubtedly the outcome of a misconception of the function of the lower one, or two, of Houston's valves. Although Houston was perfectly right in regarding these transverse folds as a part of the normal structure of the rectum, yet it is only within the last few years that they have

¹ Communicated to the Astronomical Society of Great Britain and Ireland, June 1897.

been regarded as something more than of exceptional occurrence, and their significance appreciated.

The early writers on anatomy gave the name *rectum* to the lower portion of the large intestine because its external surface appeared to be smooth and even, devoid of the constrictions or sacculations which characterise the colon, while at the same time it seemed to be surrounded with a uniform layer of longitudinal muscular fibres. That this conception of the structure of the rectum, which is accepted by most anatomists at the present day as its chief distinctive feature, is an erroneous one, I am convinced, from a large experience in examining and comparing recta from individuals of all ages. To substantiate this statement I beg to submit the following observations.

The *external surface* of the rectum is not perfectly smooth and even, but on the contrary is, as a rule, indented on its lateral surfaces alternately by a varying number of partial constrictions or inflections, which project as sharp and ineffaceable edges into its interior. Although there is much individual variation in regard to these external inflections, some recta showing none at all, still the majority have as many as three or four, while some may have as many as five, six, or seven. The two or three lower constrictions, which are the most striking, are generally associated with a slight flexure in the axis of the bowel, which gives to the rectum a more or less sinuous appearance. All the coverings of the intestinal wall participate in the formation of these constrictions, except near the median line in front and behind, where the longitudinal muscular fibres often pass directly over them.

The *longitudinal muscular fibres* of the rectum, although they form an uninterrupted layer of considerable thickness, yet are not distributed over its surface in uniform layer, but are perceptibly thicker and shorter on its anterior and posterior surfaces than on its lateral surfaces. The thicker and shorter fibres on the anterior surface are the combined fibres of the two free *tæniæ* of the sigmoid flexure, while the thicker and shorter fibres on the posterior surface are the fibres of the *tænia mesenterica* continued into the rectum, which here, as in the *flexura*, are generally shorter and more developed than those on the anterior surface. This arrangement of the longitudinal fibres I

have determined from numerous macroscopic preparations, both wet and dry, and also from microscopic sections of both contracted and dilated recta. The want of uniformity in the distribution of the longitudinal muscular fibres, and the inequality of their length, is analogous to the arrangement of longitudinal muscular fibres of the colon into bands or *tæniæ*, which are shorter than the intervening intestinal wall. For the same reason, I consider that the thicker portions of the longitudinal muscular fibres on the anterior and posterior surfaces of the rectum, which are shorter than the intervening longitudinal fibres, are in reality *tæniæ recti*.

In the colon the constrictions on its external surface, together with their internal projections, are due to the shortness of the *tæniæ*; in like manner, the constrictions on the sides of the rectum, together with their internal projections (Houston's valves), are due to the shortness of the anterior and posterior longitudinal muscular fibres. As the principle is the same in both instances, then the rectum, like the colon, must be regarded as having a sacculated structure. The colon having three *tæniæ*, consequently has three rows of sacculi: it follows, therefore, that the rectum having two *tæniæ* should have two rows of sacculi, which is the case, one on each lateral surface.

Comparing a large number of distended recta, a considerable variation in form will be noticed, depending on the distribution of the longitudinal fibres. The more uniform the distribution, the straighter the rectum; the more prominent the *tæniæ*, the more marked the constrictions and the sinuous appearance of the organ. It will also be observed that they incline to one typical form of alternating constrictions and sinuosities. That this form is due to the shortness of longitudinal muscular fibres in front and behind can be demonstrated on a rectum distended with air or water, by cutting these fibres at the places where the constrictions occur, the resulting elongation of the anterior and posterior surfaces being sufficient to straighten out the inflections on the sides of the rectum, and to smooth out the internal folds of mucous membrane.

Contrasting the sacculations of the rectum with those of the colon, it will be seen that in the lower half of the rectum where the inequality in the distribution of the longitudinal

muscular fibres is not marked, and where there is a marked increase in the thickness of both muscular layers, the sacculi not only alternate, but are associated with a slight flexure in the axis of the gut as well; in the upper half of the rectum, where the inequality in the distribution of the longitudinal fibres is more evident, and where both muscular coats are thinner, the sacculi, as a rule, alternate, but the alternation is not accompanied with a flexure. In the colon, where the distribution of the longitudinal fibres is most unequal, and where the intervening intestinal wall is much thinner, the sacculations follow in quick succession, alternating, as a rule, when two adjoining rows are compared together, but are entirely independent of any flexure in the axis of the gut. In the rectum, however, owing to the thickness of the intestinal wall, the sacculations cannot follow one another so rapidly; consequently, the sides of the gut, in adjusting themselves to the drawing or gathering action of the *teniae*, are thrown into large, alternating sacculi. In both colon and rectum the circular muscular fibres are accumulated in larger numbers at the places where the constrictions occur: this is particularly noticeable in the rectum, where the bundles of circular fibres are drawn or crowded together into prominent ridges, at the same time puckering up the mucous membrane directly in contact with them into deep transverse folds.

From these observations I draw the following general conclusions:—

First, that in an intestine having the same general character as the upper part of the rectum, with two *taeniae* placed on opposite surfaces, the action of the *taeniae* will produce a folding in of the intervening surfaces, first on one side, then on the other,—*i.e.*, alternating sacculi.

Second, that in an intestine with a greater development of both muscular layers, as in the lower half of the rectum, where the two *taeniae* are not well marked, owing to the development of the intervening longitudinal fibres, the action of the *taeniae* will produce alternating sacculi, accompanied with a flexure, the flexure depending on the greater thickness of the intestinal wall.

Third, that in an intestine with no *taeniae*, but with a perfectly

uniform layer of longitudinal muscular fibres, with no inequality in their length, the result would be an even cylindrical tube, a condition that does not exist in the rectum, but one that can be readily produced by destroying the action of the anterior and posterior longitudinal fibres, by the simple procedure of cutting them at the places where the constrictions occur.

This, it seems to me, is the correct explanation of the constrictions and transverse folds occurring on the sides of the rectum, that have been so often noticed and described, and considered by some as mere inflections, due to the bending of the rectum from one side to the other.

ABNORMAL RELATION OF THE VERMIFORM APPENDIX TO THE PLICA VASCULARIS, LEADING TO APPENDICITIS. By H. D. ROLLESTON, M.D., F.R.C.P.,
Senior Assistant Physician and Lecturer on Pathology at St George's Hospital.

THE following condition of the vermiform appendix was found during the post-mortem examination of a boy aged 6 years, who had been run over and had sustained extensive head injuries.

The appendix was $4\frac{1}{2}$ inches long, and came off in about its normal position from the left side of the cæcum. It was provided with its mesentery, and formed a fan-like curve towards the left. This part of the appendix contained a considerable quantity of soft faecal material. The appendix then turned to the right, and ran through the plica vascularis (Lockwood), at which point it was bent on itself and presented a narrowed lumen. The distal portion was somewhat distended, and was attached by adhesions, manifestly due to past inflammation, to the larger right pouch of the cæcum on its outer side. On opening this terminal portion of the appendix it was found to contain a date-shaped enterolith, which was firm and fairly dry.

This specimen is interesting, both from the anatomical and from the pathological points of view.

The plica vascularis is the name applied by Lockwood¹ to that part of the fold of peritoneum or mesorchium which is reflected over the spermatic vessels, and extends from the back wall of the abdomen to the testis, while the inferior part of the mesorchium which contains the testicular end of the gubernaculum testis is called the plica gubernatrix.

In this specimen the plica vascularis was well marked, and was attached above to the cæcum and vermiform appendix. Below, it passed into the peritoneum covering the psoas muscle, and lay over the spermatic vessels. The distinctness of the plica

¹ *Trans. Royal Medical and Chirurgical Society*, vol. lxi. pp. 502, 503.

vascularis has been accentuated (*vide* drawing) by pulling the cæcum upwards, and so putting this fold on the stretch.

The upper end of the plica vascularis on the right side may end either upon the vermiform appendix, the mesentery, cæcum, or



Drawing showing the Vermiform Appendix passing through the Plica Vascularis.
The termination of the Appendix is inflamed and adherent to the Cæcum.

ileum.¹ In this case there was an attachment to the vermiform appendix and to the cæcum, but the anatomical interest is that

¹ Wrisberg, quoted by Lockwood.

the appendix later on passes through the plica vascularis. At this point the appendix is somewhat bent on itself, and its lumen is narrowed.

This narrowing has an important pathological bearing. The proximal portion of the appendix contained soft faeces, which could, especially when the intra-appendicular pressure was increased, either from muscular contraction or faecal accumulation in the caecum, trickle through the obstruction into the distal portion of the appendix. But once there, the faecal material was probably unable to return, and remaining there, gradually became more solid by the absorption of its more fluid elements by the walls of the appendix, and so a faecal concretion resulted. This, by setting up catarrhal appendicitis, produced the peritoneal adhesions which united the terminal part of the appendix to the right side of the caecum.

This passage of the appendix through the plica vascularis gave rise to torsion, narrowing of the appendix at that point, and eventually to appendicitis, and is an example of the causation of appendicitis by torsion described by Mr Treves.

It might be thought, perhaps, inasmuch as there were peritoneal adhesions around the tip of the appendix, that the fold of peritoneum described as the 'plica vascularis' was only another pathological adhesion. This, however, is not supported by the character of the fold, which is distinct and free from any general adhesions to surrounding parts. In addition, it is situated in the normal situation of the plica vascularis, as shown by the spermatic vessels.

The drawing, for which I am indebted to Mr E. Wilson, B.A. Cantab., of St George's Hospital, shows the caecum drawn upwards and to the right, with the proximal portion of the appendix containing soft faeces lying on its under surface, the appendix with its mesentery, the narrowed and bent condition of the appendix where it passes through the plica vascularis, and its dilated termination united by peritoneal adhesions to the caecum.

**CASE OF MARKED DISTENSION OF THE TRANSVERSE
AND DESCENDING PARTS OF THE COLON.¹ By
ROBERT HOWDEN, M.A., M.B., *Professor of Anatomy in the
University of Durham.***

THE following conditions were found in an adult male subject dissected in the University of Durham College of Medicine, Newcastle-upon-Tyne, during the winter session 1896-97.

The abdominal wall exhibited no marked distension, while its muscles and vessels were found to be quite normal. On opening the abdominal cavity, what looked like an enormously distended stomach presented itself to view, and was seen to occupy the whole of the epigastric and umbilical areas, together with a considerable portion of the right and left hypochondriac regions. On further examination, this distended viscus proved itself to be the transverse colon, which was bound to the diaphragm by a greatly expanded phrenico-colic ligament,—this last being attached to the diaphragm along a line extending from the ensiform cartilage to the 10th rib, at an average distance of about 2 inches (5 cm.) above the left costal margin. On dividing the anterior part of this ligament and drawing down the distended colon, the previously hidden stomach was exposed. This was found to be dilated—measuring 25 inches (about 63 cm.) along its greater, and 9 inches (23 cm.) along its lesser curvature.

The spleen was of normal size, and was placed deeply in the left hypochondriac region,—its anterior extremity being distant about 3 inches (7.6 cm.) from the tip of the 11th rib. The liver was crushed into the right hypochondriac region—the entire organ lying to the right of the vertebral column. The anterior margin of the left lobe looked directly forward, and occupied a vertical position. The under surface of this lobe was directly towards the left, and deeply indented by the stomach. The lower margin of the right lobe reached the level of the

¹ Read at the meeting of the Anatomical Society of Great Britain and Ireland. Dublin, June 1897.

posterior part of the iliac crest, and the fundus of the gall-bladder projected below the costal margin, opposite the anterior extremity of the 11th rib. The falciform ligament was stretched, and extended obliquely from its diaphragmatic attachment towards the right side, in order to reach the liver. Its free margin measured 6 inches (15 cm.), whilst its vertical measurement was 7 inches (nearly 18 cm.). The lower end of the right kidney was on a level with the iliac crest; the left occupied its usual position. The diaphragm on the left side reached as high as the lower margin of the 2nd rib, in the line of the nipple; on the right side its upper limit corresponded with the lower border of the 4th rib, in the same line.

There was no trace of a great omentum below the colon, but the appendices epiploicæ were fairly well marked. Between the greater curvature of the stomach and the upper aspect of the colon the omentum had a width of 4 inches (10 cm.). The right gastro-epiploic artery sent numerous branches downwards to the anterior surface of the distended colon. The cæcum and vermiform appendix were not displaced. The ascending colon was of an average calibre, and exhibited the longitudinal tæniæ and the usual sacculations. The posterior tænia could be traced over the hepatic flexure on to the posterior surface of the distended transverse colon, where it could be seen and felt as a distinct band. The omental tænia, on the other hand, was lost a short distance beyond the hepatic flexure.

The colon was moderately inflated from the lower part of the ileum, and the accompanying photographs give different views of the abdominal viscera under this condition.

Photograph No. 1. — View of the abdominal viscera from the under and left aspects—the distended colon having been drawn slightly upwards over the costal margin.

No. 2.—View of the viscera from the front—the body having been suspended by the neck. Here also the distended colon has been drawn slightly upwards over the costal margin.

No. 3.—View from the right side—the distended colon having been drawn downwards in order to show the dilated stomach.

The transverse colon presented the form of a large bilobulated sac, which communicated freely with the hepatic and splenic flexures. Of the two pouches, the lesser was placed on the right side of the middle line, and occupied mainly the right hypochon-

PHOTOGRAPH No. 1.—*View of Viscera from below.*

P. C., Descending colon.
S. P., Mucous flexure.
P., Sigmoid flexure.

C., Cecum.
T. C., Transverse colon.
S. P., Mucous flexure.

PHOTOGRAPH No. 2.—*View of Viscera from the FRONT.*

<i>C</i> , Cæcum.	<i>T.C</i> , Transverse colon.	<i>S.F</i> , Splenic flexure.
<i>D.C</i> , Descending colon.	<i>S.F</i> ¹ , Sigmoid flexure.	<i>I</i> , Intestinal coils.

PHOTOGRAPH No. 3.—View of Viscera from RIGHT SIDE.

G, Gall-bladder.

T.C, Transverse colon drawn downwards.

St, Stomach.

driac region, while the larger lay in the epigastric, umbilical, and left hypochondriac areas. The splenic flexure was firmly bound to the diaphragm by the phrenico-colic ligament, and presented a slight indentation which marked it off from the succeeding descending colon. This last was markedly funnel-shaped, being dilated superiorly and narrowing inferiorly so as to reach something like its normal calibre on reaching the left iliac fossa.

The following measurements will assist in giving some idea of the size of the viscus, viz.—

1. Length from hepatic to splenic flexure, measured along its upper margin, 34 inches (86 cm.).
2. Circumference of transverse colon immediately to the left of the hepatic flexure, $14\frac{1}{2}$ inches (37 cm.).
3. Circumference of lesser dilatation of transverse colon, $23\frac{1}{2}$ inches (59.5 cm.).
4. Circumference of greater dilatation, 29 inches (73.5 cm.).
5. Circumference of the splenic flexure, $20\frac{1}{2}$ inches (52 cm.).
6. Circumference of the highest part of the descending colon, 20 inches (50.8 cm.).

The ascending, transverse, and descending parts of the colon were removed *en masse*, and carefully washed out. Their contents consisted merely of a small quantity of mucus; there was no hypertrophy of the muscular coats of the gut. They were then placed in a large trough and filled with water, the trough being filled from a second tap at the same time that the gut was being distended, in order to support the latter and prevent its rupture. The water inside the viscus was carefully drawn off, and was found to measure just over 20 litres (*i.e.*, about $4\frac{1}{2}$ gallons); the average normal capacity of the same parts of the large intestine, measured in a similar manner, being from 3 to 4 litres. The sigmoid flexure and rectum were carefully examined, but no trace of a stricture could be detected; the former was empty, while the latter contained a small quantity of pultaceous faeces.

In order to localise, as far as possible, the position of the thoracic viscera, the body was placed in the supine position, and a number of sharp, stiff steel needles were driven through the chest at different points. The anterior part of the chest-wall was then carefully removed, when the following facts were ascertained, viz.—

1. Both lungs were fixed to the chest-wall by dense pleuritic adhesions.

2. The left lung extended for a distance of 2 inches (5 cm.) to the right of the mid-sternal line at the level of the upper margin of the third costal cartilages.

3. The diaphragm, as already stated, reached on the left side as high as the lower margin of the second rib in the nipple line, while on the right side its highest level corresponded to the lower border of the fourth rib.

4. The pericardial sac, at the level of the upper border of the 4th costal cartilage, extended transversely from a point $\frac{1}{2}$ an inch (1.25 cm.) to the left of the mid-sternal line, to one $3\frac{1}{2}$ inches (9 cm.) to the right of the same line.

5. The heart lay almost entirely to the right of the mesial plane of the body,—a needle driven through the middle of the sternum opposite the fourth costal cartilages transfixing the wall of the left ventricle. The upper part of the interventricular furrow corresponded to the junction of the right third and fourth costal cartilages with the sternum.

6. The pulmonary valve was on a level with the right second costal cartilage where it joined the sternum. The aortic and mitral orifices were transfixed by a needle, which had been passed through the chest at the upper border of the right third costal cartilage close to the sternum. The valves of the heart appeared to be healthy.

7. The distance from the upper border of the neck of the first rib on the left side to the highest level of the diaphragm on the same side was $4\frac{1}{2}$ inches (11.4 cm.).

Cases of dilatation of the colon, not secondary to any organic change, have been divided by Rolleston and Haward (*Clinical Society's Transactions*, vol. xxix.) into two classes:—

1. *Acquired*, which develop some time after birth or in adult life. They are generally directly referable to constipation, and the dilatation is more or less local as a rule, the distension being most marked in the sigmoid flexure, and gradually diminishing towards the cæcum. . . .

2. *Congenital*.—Cases where the distension comes on soon after birth, and where the bowels have never acted naturally. The distension and dilatation of the colon are more general, and,

probably from their longer duration, more marked. Constipation seems to be the result of inactivity or atony, and not to be the primary cause of the distension. But it must be admitted that a hard-and-fast line cannot be drawn between congenital cases where the constipation is secondary, and the commoner cases of acquired dilatation of the colon directly due to constipation. They give the history of a case in a boy who died at the age of 12 years, and who, from early youth, had been the subject of gradually increasing constipation,—he having once gone for nine weeks without an evacuation. After death the descending colon and sigmoid flexure were seen to be greatly distended, while the first part of the rectum was dilated to a lesser extent. They quote numerous references to other recorded cases, and discuss the different theories as to the causation of this condition. Unfortunately, in the case which I have just described, the identity of the subject could not be established, and so a clinical history was not obtainable.

The following facts regarding it may, however, be summarised, viz.—

1. The absence of any apparent abdominal distension, and of any trace of a stricture on the distal side of the dilatation.
2. The distension was entirely above the sigmoid flexure,—this, together with the rectum, being of ordinary calibre.
3. The wall of the distended portion of the gut showed no trace of hypertrophy.
4. The marked effects on the neighbouring viscera would point to the dilatation as having existed for some very considerable time.

The specimen is now preserved in the museum of the University of Durham College of Medicine, Newcastle-upon-Tyne.

PHOTOGRAPH No. 4.

View of colon from its anterior aspect—the viscus having been removed from the body, inflated and dried. Its original shape and curvature have been to some extent lost, but the photograph shows well the relative proportions between the ascending colon of normal diameter and the succeeding dilated portions of the gut.

I, Lower end of ileum.
T.C, Transverse colon.

C, Cæcum.
S.F, Splenic flexure.

A.C, Ascending colon.
D.C, Descending colon.

ON A PAIR OF NEGRO FEMORA.¹ By THOMAS H. BRYCE,
M.A., M.B., *Lecturer on Anatomy, Queen Margaret College,
University of Glasgow.*

IN a recent number of this *Journal* I published some "Notes on the Myology of a Negro." The pair of femora which form the subject of the present paper belonged to the same individual, and I purpose to describe the characters of the bones, in their relation to certain muscular arrangements described in my former paper, and to discuss certain analogies between them and the celebrated Trinil femur.

Right femur.—The upper end of the bone is much deformed by chronic rheumatic arthritis. The head is irregular, and its articular surface eburnated; the neck and trochanter major, as well as the subtrochanteric region of the shaft, are much thickened by the irregular deposit of new bone. The rest of the shaft and the lower extremity show no signs of pathological change.

The linea aspera is somewhat prominent, giving a pilasteric index of 109·2,—rather below the average for negro bones given by Hepburn.² The bicondylar width is 82 mm. The intercondylar notch is narrow, and the curvature of the condyles is considerably sharper than in a European bone. The back of each condyle shows an accessory facet.

The popliteal surface measures 11 cm. in height. The external supracondylar ridge is prominent; it attached a strong accessory fasciculus of the biceps, which passed from the long head to the femur. The internal supracondylar ridge is only slightly marked, while running down the space between the two lines is an oblique ridge, which gave attachment to the femoral head of the biceps. This ridge commences close to the internal supracondylar ridge above, but ends below in the

¹ Read at the meeting of the Anatomical Society of Great Britain and Ireland, June 10, 1897.

² *Jour. Anat. and Phys.*, vol. xxxi. part 1, Oct. 1896.

middle line 4 cm. above the condyles. Below this level there is a prominent mesial convexity running down to the intercondylar notch, bounded on each side by a supracondylar hollow.

The general effect is to give the popliteal surface a convex contour, which is expressed by the following measurements, taken at a point 4 cm. above the highest point of the external articular surface, on the front of the bone (Manouvrier's 4 cm. line).¹ The antero-posterior diameter *mp*—that is, with the posterior limb of the callipers resting on the most prominent point of the popliteal surface—is 31 mm., while the diameter *mn*—the posterior point being taken on the external supracondylar ridge—is 30 mm. The transverse diameter is 36 mm., giving the high popliteal index of 86·2. There is no suspicion of pathological change here, the convexity being due to the presence of the ridge which gave attachment to the femoral head of the biceps.

Left femur.—The total oblique length is 470 mm., just about the average given by Hepburn;² the diameter of the head is 52 mm. The subtrochanteric region of the shaft shows some degree of flattening. The antero-posterior diameter is 23 mm., the transverse 32·5 mm., giving a platymeric index of 70·7, considerably below the average (77·7) given by Hepburn for nine Negro bones. The anterior part of the shaft is here somewhat concave, due chiefly to the projection of the internal border, which rises into a prominent ridge opposite the lesser trochanter, but fades away again at the junction of the upper and middle thirds of the shaft. The spiral line runs into this ridge in front of the lesser trochanter, and is not continued upwards as the anterior intertrochanteric line. The latter is only faintly marked, the concavity of the anterior part of the shaft being continued up on to the neck of the bone. The outer border or external infratrochanteric ridge (Turner)³ is rounded. The projection of the linea aspera is not very marked,—the antero-posterior diameter is 29 mm., the transverse 28·5 mm., giving a pilasteric index of 101·7. Thus there is a low pilasteric associated with a somewhat low platymeric index; whereas, according

¹ Manouvrier, "Deuxième étude sur le *Pithecanthropus erectus*," *Bull. de la Soc. d'Anthrop. de Paris*, tome sixième, 1896, fasc. v. (iv^e série).

² *Jour. Anat. and Phys.*, vol. xxxi. part 1, Oct. 1896.

³ *Challenger Reports*, part xlvii. p. 97, and *Proc. Scot. Soc. Antiq.*, May 1895.

to Manouvrier, a low platymeric is generally associated with a high pilasteric index. In the middle section of the shaft the hollow for the vastus externus is well marked, but there is no corresponding pilasteric excavation for the vastus internus, so that the inner face of the shaft is convex for the whole of its extent. It has been suggested that subtrochanteric flattening is due to increased development of the upper portion of the crureus and vastus internus (Manouvrier), or that this portion of the bone is modified in shape by its being acted on by the opposing forces of these muscles and the gluteus maximus (Hepburn), the forces coming into action in the muscular effort of walking in a mountainous country. The degree of flattening in this bone is not sufficiently marked to test completely this hypothesis, but it is interesting to note, in connection with it, the arrangement of the muscles supposed to be concerned. The gluteus maximus was a powerful muscle, but attached just as usual; there is no third trochanter, and the lower part of its impression is a hollow, not a raised ridge, and placed on the posterior aspect of the bone. The vastus externus was very well developed, and could not be separated from the crureus below, but above it came separately from the tubercle of the femur, and the shaft in front of and below the great trochanter, as usual. The crureus and vastus internus were inseparable above, but the latter was regarded as being confined to the inner face of the bone, behind the prominent inner border, while the upper part of the crureus, which was better developed than is usual, arose from the hollowed-out anterior surface of the shaft and anterior intertrochanteric line.

The bicondylar width is 82 cm., and the intercondylar notch is narrower even than on the right bone, and the sharp curvature of the condyles, especially of the external, is striking (fig. 3).

The popliteal surface extends 11 cm., 4 mm. above the condyles; the external and internal supracondylar ridges are prominent, and supported by bony pillars or buttresses. Each rises above into a spine; the outer of these spines attached the accessory fasciculus of the biceps, the inner forms the upper end of a prominent oblique ridge, which passes downwards on to the popliteal surface. This ridge is interrupted below, but in a line

with it, in the middle of the space, and 4 cm. above the condyles, is a prominent tuberosity. The spine, ridge, and tuberosity attached the femoral head of the biceps, and a vessel passed outwards, under that muscle, at the point where the ridge is interrupted.

Below, and internal to this tuberosity, is another for the inner tendinous head of the gastrocnemius, which was very strong and extended over the whole inner half of the popliteal space,

FIG. 3.

coming in contact above with the lower part of the short head of the biceps.

Instead, therefore, of the smooth, slightly concave surface which usually characterises the popliteal portion of the femur, we have an irregular projecting surface, which at first sight is suggestive of a pathological process; but it is to be noted that the whole of the popliteal surface was in this case covered by muscular attachments, and that the ridges and tuberosities are not casual exostoses, but were definitely associated with the tendinous origins of certain muscles. Expressing the facts in

figures, we find that at the 4 cm. line $mp=37$ mm.; $m.n.=35$ mm.; *transverse*=40 mm.; giving a popliteal index of 92.5.

The pair of femora above described present a double analogy to the Trinil fossil,—1st, in respect of the signs of a pathological process associated with the formation of exostoses: 2nd, in respect of certain characters which are common to both, though they may not be present in the same degree. Dubois claimed that the fossil was unique in the possession of three characters—a concave anterior intertrochanteric line, a convex internal surface, and a convex or rounded contour of the popliteal surface.

Manouvrier¹ and Hepburn² have, however, shown that all these three characters may be present in certain rare specimens, in the large collections of human femora examined by them. With regard to the first two characters there is no dispute. They are present in many femora as well as in the pair which are the subject of this paper, but there has been considerable discussion as to the convexity of the popliteal space.

Many regard the feature in the fossil as a pathological one, but both the observers above named have described femora which approach closely the fossil in this respect, and are yet free from the suspicion of being pathological. In explanation of the convexity of the popliteal surface, Manouvrier¹ has suggested that the bone retains its cylindrical character to a lower level than usual, owing to the descent of the vastus externus. Hepburn,² with more probability I think, suggests that the popliteal surface in these cases has been occupied by muscle. He further suggests, from his observations on the limbs of the anthropoid apes, that the adductor magnus may descend further than usual, and he desires information as to origin of the femoral head of the biceps in the lower races of men.

In this instance I have been able to demonstrate that in the right bone, without any suspicion of its being pathological, the convexity of the popliteal surface is due to the presence of a ridge from which the femoral head of the biceps arose, while in the left bone the impression for that muscle, and for the inner head of the gastrocnemius are marked by bony prominences. The development of the spine and crest in the upper part

¹ *Loc. cit.*

² *Loc. cit.*

of the tendinous origin of the short head of the biceps is an instance of the very process suggested by Sir Wm. Turner as explaining the exostosis on the Trinil femur. The Negro was the subject of a disease associated with the formation of periosteal nodes, and both tibiæ showed irregular exostoses due to this cause. It does not follow, however, that the exostoses on the popliteal space are necessarily pathological, for they are strictly muscular impressions. On the other hand, the thickening of the supracondylar ridges is difficult to account for unless it be pathological, and this throws the whole open to the same suspicion.

The interest of the specimens in relation to the Trinil femur lies in this combination of the two factors, morphological and pathological; and the left bone suggests a simple and not impossible hypothesis as to the cause of the convexity of the popliteal surface of the fossil femur.

**SKIAGRAPHY AFTER INJECTION OF THE BLOOD-
VESSELS WITH MERCURY.¹ By HAROLD J. STILES,
M.B., F.R.C. Ed., *Senior Demonstrator of Surgery, University
of Edinburgh.* (From the Surgical Laboratory of the Uni-
versity of Edinburgh.)**

PHOTOGRAPHY by the X Rays, or Skiagraphy as it is now called, although so recently discovered, has established itself as a valuable addition to the diagnostic methods employed in medicine and surgery. Up to the present, anatomists have made little use of it, mainly from the fact that the shadows cast by the viscera are not sufficiently well defined.

At a conjunct meeting of the Scottish Branches of the British Medical Association, held in Edinburgh on the 5th February of this year, Dr Nathan Row of Dundee showed some skiagraphs taken after injection of the arteries with a coloured plaster solution. These photographs were particularly interesting to me, because, before seeing them, I had intended to ascertain what results could be obtained by employing mercury for the same purpose. Mercury naturally suggested itself to my mind, firstly, because the older anatomists employed it with so much success for injecting the lymphatics; and secondly, because, being a pure metal, I thought it would cast a shadow deep enough to show up against the bones, in the same way that a bullet does. I am indebted to the Medical Supply Association for taking the skiagraph here reproduced. It gives the result of my first experiment,—a result which I venture to think is sufficiently encouraging to warrant my directing attention to it. It was taken from the right arm which I had removed from a child aged 4 years, on account of tubercular disease of the elbow, which was too advanced for excision. Shortly after the operation a small cannula was tied into the brachial artery; a piece of rubber tubing, about two feet long, was attached by one end to the cannula, and by the other end to a glass funnel; the

¹ Read at the meeting of the Anatomical Society of Great Britain and Ireland, Dublin, 1897.



FIG. 1.

funnel was then elevated above the level of the limb, and mercury gradually poured into it. By elevating the mercury to a height of two or three feet, it could be made to spurt out for a considerable distance from the divided vessels at the amputation surface. At first, it seemed doubtful if the injection had been successful, as only about 10 c.c. of mercury was retained in the limb. On making a small skin-deep incision into the point of the ring finger, minute lobules of mercury escaped, thus showing that the mercury had reached the smallest vessels. Before taking the skiagraph, the limb was interposed between the X rays and the screen, with the result that deep shadows of the vessels were distinctly seen. The photograph shows that even the smallest vessels have been revealed, and that mercury gives infinitely better results than plaster of paris. With a coil giving an 8-second spark, it was found that an exposure of 90 seconds showed the vessels very distinctly, but not so the bones, which were over-exposed. In this particular specimen an exposure of 45 seconds gave the best results. To show the arteries distinctly in the adult, a longer exposure is necessary, in order to diminish the depth of the shadows cast by the bones, and so as not to obscure the vessels. In this hand, the radial artery does not appear to have given off, either directly or indirectly, any definite branch to complete the superficial palmar arch; indeed, an arch can hardly be said to exist. The digital branches might be described as the result of three bifurcations,—first of the trunk, then of its external division, and finally of the external division of the second bifurcation. The writer cannot help thinking that the classical description of the ulnar artery in the palm applies only in the minority of cases. In those instances in which the 'arch' is completed by the radial, the anastomosing branch, as a rule, is not only small, but very variable as to its mode of origin. The *superficialis volæ*, although larger than usual, has, in this instance, no connection with the ulnar, and appears to end in the muscles of the thumb. The deep branch of the ulnar arises, as is not infrequently the case, from the digital branch to the little finger. In point of size and direction, it would appear that the *arteria princeps pollicis* has more right to be regarded as the continuation of the radial than has the deep arch. The loop

which the *arteria princeps pollicis* exhibits as it lies in the web of the thumb is possibly a provision for preventing undue stretching of the vessel when the thumb is fully abducted; no such loop is seen in the photograph taken with the thumb in the latter position. It must be left, however, to other specimens to show whether this looping of the vessel is a constant condition. We know that something very similar occurs at the elbow, and possibly also at the knee. The rich blood supply to the pulp of the fingers and the matrix of the nails is well seen. I would draw attention also to the two collections of mercury which are situated a little above the wrist. At first sight these might be taken for accidental extravasations, but closer inspection shows that the mercury is confined to the lower ends of the diaphyses of the bones of the forearm. This is of interest when we remember how actively growth takes place in this situation during childhood. This high degree of vascularity, combined with the slowness of the circulation, is, as is well known, the explanation usually given for the frequent occurrence of tubercle in the extremities of the diaphyses of growing bones. The photograph certainly appears to lend support to this explanation. The vascular loops which the vessels form on the diaphysial side of the epiphysial cartilage are not only very large, and reduced to a single layer of endothelium, but they are also very badly supported, so that it is quite possible that some of them may have given way. Although the skiagraph has been taken from a child's limb, it is to be hoped that equally good results may be got in adults by prolonging the exposure.

The writer is not without hope that the employment of the X rays to parts which have been injected with mercury will prove of service to those engaged in the teaching of surgical anatomy and operative surgery. As regards the arteries, their general course, their branches and anastomoses, and their relations to the surface are well brought out. It seems also that this method opens up to the anatomist a field of investigation worthy of his attention. An attempt should be made to record the position of the various organs by skiagraphy, after injecting their blood-vessels with mercury: such organs as the spleen, kidneys, etc. ought to lend themselves to this method of investigation; and perhaps also some of the hollow viscera

could be dealt with in the same way. Mercurial injections of the lymphatics ought certainly to be photographed by the X rays, as it is possible that in this way more light might be thrown upon the paths of lymphatic dissemination in cancer. The appearances presented by effusions into the larger joints could readily be stimulated and recorded by filling the synovial cavities with mercury, although probably the weight of the metal would somewhat modify the appearances. But it is useless to mention further directions in which such investigations may be pursued; they are sure to suggest themselves to those who are interested in the matter.

ADDENDUM

Since the above was written, I have been fortunate enough to secure the co-operation of my colleague Dr Harry Rainy, who has taken the skiagraphs of the injections I have made. These may be classed into three groups:—1st, Injections of the arteries of the limbs; 2nd, of the vessels of certain viscera; 3rd, of the trachea, ureter, etc.

Before describing the individual photographs, a word or two is necessary regarding the precautions which must be taken in making the injections.

(1) The blood should be thoroughly washed out of the vessels before introducing the mercury.

(2) Specimens which it is not convenient to photograph within a day or so after death, should, before introducing the mercury, be preserved by injecting the vessels with a 5 per cent. solution of formalin.

(3) The part to be photographed should, whenever possible, be placed in the position in which it is to be photographed before introducing the mercury. If this point is not attended to, the column of mercury in the vessels is liable to be interrupted by subsequent movement of the part, as may be seen in the photograph of the thigh.

(4) If the part is to be photographed in several positions, it should be moved as gently as possible. As mercury, like every mobile fluid, passes readily through the capillaries, means must be taken to prevent the veins being injected as well as the

arteries. This may be done by making a small skin-deep incision at the extremity of one of the digits; and the moment the mercury appears at the cut, the injection should be stopped. Neglect of this precaution in one of the earlier injections gave rise to the appearance shown in specimen 2.

(5) The pressure must be moderate, and should not, in ordinary circumstances, exceed 30 mm. of mercury.

FIG. 2.

(6) The best photographic results are obtained by exposures somewhat longer than those required in clinical work.

Photograph No. 3 is taken from a child aged $2\frac{1}{2}$ years, in whom the anterior abdominal wall, the stomach, the liver, and the small intestine had been removed. The injection was made from the abdominal aorta. On the left side the column of mercury has been extensively interrupted in several places, in consequence of the body having been moved about on various

occasions between injecting and photographing it. In interpreting the appearances shown in this photograph, it must be remembered that the structures revealed are merely shadows cast upon one plane, so that vessels which cross must not be considered as anastomosing; but after allowing for this, it is very obvious that a very free communication exists between the branches of the larger trunks. The photograph illustrates very forcibly the anastomoses which would be concerned in carrying out the collateral circulation after ligature of the various main vessels: for example, the anastomoses between the branches of the internal iliac and those of the profunda are well brought out, and they show how the collateral circulation would be brought about after ligature of either the external iliac or the common femoral arteries.

Photograph No. 4 (child, æt. $2\frac{1}{2}$ years) is of interest as showing the considerable interval which exists between the popliteal artery and the trigone of the femur, when the leg is flexed. It also shows what a gradual curve the vessel makes at the knee, thus contrasting with the loop already referred to upon the *arteria princeps pollicis* at the web of the thumb.

Photograph No. 5, from the same limb, shows the level of the bifurcation of the popliteal artery and of the origin of the peroneal. The way in which the anterior tibial artery passes in the first instance forwards to gain the front of the interosseous membrane is to be noted, as it explains how it is that the vessel is so liable to retract behind that membrane in amputating the leg at the seat of election. The relation of the same artery to the tibia is well shown.

In Photograph No. 6 (child, æt. $2\frac{1}{2}$ years), the renal artery was injected on the right side, and the ureter on the left. The form, size, position, and axis of the kidney are shown, as also is the dendritic plan of its blood supply (fig. 2). The relatively large size of the organ in the child is shown by the fact that it reaches from the upper border of the 12th dorsal vertebræ to the lower border of the 3rd lumbar. Its long axis is almost vertical instead of being oblique, as is the case in the adult. The hilum is opposite the lower border of the 1st lumbar vertebra. The centre of the pelvis of the left kidney is opposite the upper border of the 2nd lumbar vertebra, just below the tip of the

demonstrating the ramifications of the bronchial tree. Where the lungs are healthy, the mercury has found its way to the alveoli, and has produced a uniformly black shadow. In the diseased portions of the lung the inflammatory exudation has limited the injection to the bronchial tree and the infundibula. The bifurcation of the trachea is seen at the level of the 4th dorsal vertebra, the root of the left lung at the level of the 5th. The regularity of the lower border of the right lung is to be noted; it is seen to extend down to the level of the angle of the 11th rib. The sharp and straight outline made by the posterior border of the lung is somewhat striking.

We think these experimental results are sufficiently encouraging to warrant further work along the same lines.

ON A FUNCTIONAL ADAPTATION OF PHAGOCYTOSIS.¹

By Dr C. DE BRUYNE, Ghent.

THE results of many observations, undertaken by different anatomists, have conclusively proved that the white corpuscles of the vertebrates can permeate the investing tissues, and can make their way by amœboid movement on to the external or internal surface of the body. These facts are so generally recognised that they scarcely constitute a matter of dispute.

I have studied analogous phenomena in certain invertebrates, more particularly in lamellibranch molluscs. In these animals the mucous covering of the gills contains a considerable number of leucocytes, which have for the greater part lost their normal appearance. It has been my endeavour to ascertain by what means these leucocytes have attained this situation. I have already published the results of a large series of experiments,² in which I have been able actually to observe the sortie of the leucocytes through the ciliated epithelium forming the superficial covering of the gills. This examination *in vivo* has furnished me with results which fully confirm those obtained *post-mortem* in the vertebrates by other observers.

The larger number of the leucocytes thus permanently quitting the body of the lamellibranch are carriers of waste products, which are very diverse in nature (histolytic residues, urinary concretions, etc.). In the particular case of the green oyster of Marennes, the inclusions of the leucocytes are tinted green by the substance diatomine, termed marennine by Prof. Ray Lankester, derived from the diatom *Navicularia ostrearia*, on which the animal more especially feeds. The leucocytes, transformed into phagocytes, are continually arriving on the surface of the gills, carrying outside the body substances which are either harmful, or more or less useless to the organism. In the course of my experiments I

¹ Read at the meeting of the Anatomical Society of Great Britain and Ireland, Dublin, 1897.

² "Contribution à l'étude de la phagocytose," *Mémoires couronnés et Mémoires des Savants étrangers*, publiés par l'Académie royale de Belgique, T. liv., 1894 ; et *Archives de Biologie*, T. xiv., 1895.

treated *Anodonta* or *Unio* with injections of fine and insoluble powders, or I plunged them for two or three days in a weak solution (1 in 10,000) of methylene blue, and in both cases I constantly found numerous leucocytes, charged with both foreign matter and pigment, making their way towards the surface of the body, and traversing the epithelium in order to gain the superficial mucus. From the results of my experiments, I have come to the conclusion that this process must be regarded as an epuration of the tissues, and one which, under certain circumstances, may be very energetic, and of considerable importance.

The female Unionidæ of the Old World and of N. America¹ afford a lodging, by means of the interfoliary chambers of their external gills, to the fertilised eggs, which undergo a certain amount of development in this situation. During this period the embryos play the part of parasites, benefiting from conditions which are essentially favourable to their development: at a later period, after they have deserted the mother, they continue their phagocytary life in the skin of a fish.² It has been stated, however, that during this epoch of incubation the exodus of the maternal leucocytes increases largely, exceeding that which takes place at ordinary times; further, that a considerable number of these leucocytes are absolutely normal in appearance. The combined results obtained from my fresh dissections, from my sections made with the freezing microtome, and from my preparations which have been stained and fixed, have led me to the conclusion that this increase in the phenomenon is a kind of reaction of the maternal organism against the parasite; in other words, that this is a case of inflammation in the sense that Metchnikoff uses the word.³ Undoubtedly, the leucocytes thus brought face to face with the embryos, enter into a contest with them,—a contest, the different phases of which may be easily followed. The vigorous and normally formed embryos continue their development in this nutritive medium, successfully resisting the attacks of the leucocytes, and even living on their residues. On the other hand, the unfertilised eggs, together with

¹ The embryos of the Unionidæ of S. America do not inhabit the maternal gills.

² V. Faussek, *Biolog. Centralblatt*, xv. (1895), p. 115.

³ Metchnikoff, *Pathologie comparée d'inflammation*, Paris, 1892.

the feeble or abnormal embryos, succumb: they may be partially or totally devoured by the leucocytes, or are swept away with the other residues by the regular vibratile play of the cilia. This process must be regarded as one of natural selection, in which only the normal and vigorous embryos are able to maintain their existence, while the development of those which are feeble or abnormal is arrested at a very early stage.

In the case quoted above, the embryo may, as I have just described, be washed away by the currents of water caused by the movements of the vibratile cilia. If, however, they have attained a certain degree of development, this method of removal may prove ineffectual, and the embryos or their remains may persist *in situ*, and undergo there all the stages of progressive disintegration (decomposition). Obviously, such a train of circumstances will prove a source of serious trouble to the host. In such an event the defence of the mother against the parasite becomes reorganised, and the reaction enters into a new phase. The leucocytes being unsuccessful in removing the residues by absorption, group themselves about them, and so dispose themselves as to construct a complete and perfectly closed cyst. This case is analogous to that of the Rhabditis, which becomes encysted by the rapid accumulation around it of the leucocytes of its host the Lumbricus, and is thereby rendered harmless. The disintegrated embryos, thus shut up in a cystic wall, constitute with it a single mass, which plays the part of a foreign body, and the only injurious effect of which is to compress the surrounding tissues. Occasionally a large number of embryos or their remains tend to accumulate: under these circumstances a single cyst may be formed around them, and the phenomenon passes through the same stages as take place in the encystment of a single embryo.

Thus it is apparent that phagocytosis normally takes place in the tissues of the lamellibranch molluscs. Subsequently an exodus of the leucocytes takes place: they make their appearance on the surface, more particularly on the gills, constituting an epuration of the tissues. Further, at the period during which the embryos accumulate in the gill-blades, the exodus assumes enormous proportions, its functional rôle is modified, and it constitutes a reaction of the mother against the parasitic embryo.

This reaction, which involves a natural selection, has two very distinct phases,—

- (a) A successful combat of the leucocytes against the feeble or unhealthy embryos.
- (b) An encystment of these embryos when they have become too numerous, or have attained too advanced a development.

I regard this case as essentially a functional adaptation of phagocytosis.

OBSERVATIONS ON THE DEVELOPMENT AND NUTRITION OF BONE AND CARTILAGE, AND ON THE RELATIONS OF CONNECTIVE TISSUES TO EACH OTHER IN HEALTH AND DISEASE.¹ By Professor REDFERN, M.D. Lond., F.R.C.S. Eng.

I WISH to bring under the consideration of the Society certain conditions of connective tissues, especially of cartilage and bone, which I believe are not sufficiently recognised, and which point to more simple explanations of developmental and diseased actions than are usually offered.

I think it can be proved that every living tissue possesses inherent powers of maintenance; and in diseased states, of active anatomical changes, independent, for their existence at any rate, of the surrounding tissues, or on a supply of vessels and nerves. That is to say, every tissue has a power of its own to do its own work,—to maintain its healthy adult characters, or to change its texture and assume the anatomical characters of other healthy tissues, possibly those of diseased ones. Notwithstanding, when such a tissue forms part of a composite body, such as the human, it influences the other tissues, and is influenced by them, whether for the maintenance of healthy or diseased conditions.

And such tissue-power, manifested, it may be, under normal conditions by changes which go on so slowly as to be observed with difficulty, may, under altered circumstances, be exercised so rapidly, and lead to appearances so startling and different from the original, as to obscure their origin, and to have led to the changed tissues having been described as altogether new, and derived from some extraneous source.

A simple illustration will make this clear. An articular cartilage may be examined repeatedly without definite indications of its continual change, or capacity for change, being observed, but after an injury, or the occurrence of phlebitis

¹ Read at the meeting of the Anatomical Society of Great Britain and Ireland, Dublin, 1897.

after blood-letting, as in cases related by Mr Mayo and Mr Lawrence respectively, complete removal or destruction of such large cartilages as those of the ankle and knee joints has taken place within a month, or, as in Mr Lawrence's case, in 4 days. And in dogs and rabbits I found that in from 3 to 6 days the parts of costal cartilages through which a silk thread had been passed, or such as had been surrounded by a ligature, had become converted into a cellular gelatinous mass, very difficult to recognise as having been formed out of the original cartilage.

In these instances it must be remembered that the irritation was continued for some time, but when the thyroid cartilage is cut, in a case of cut throat, and in instances of fractured cartilage, the changes are so slow that for long it was doubted if such injuries were ever followed by healing. Dr Leidy, in an excellent paper on articular cartilage, in 1849, expressed himself very strongly on this point, saying, "As well almost might the two opposed surfaces of articular cartilage unite in a joint in which there is little motion as for the two broken edges of one to do so."

When I had made incisions in the articular cartilages of dogs, neither microscopic nor visual changes were manifest 7 days after, but abundant proliferation of the cells adjacent to the injured part were found after 49 days (fig. 17), and perfect fibrous union after 24 weeks (figs. 18 and 19). There is now a general admission that wounds in cartilages heal by the formation of fibrous tissue. That is to say, a cartilage like the articular is capable by its own inherent power, and without any assistance from without, of transforming its elements, cells, and hyaline substance into the corpuscles and fibres of that other form of connective tissue which we know as fibrous tissue.

I believe it is neither known nor suspected how frequently many joints in a limb undergo great abnormal nutritive changes in succession. When serious disease in one joint has led to amputation or caused death, the anxiety to determine the characters of the disease by the naked eye and a prolonged microscopical examination often leads to the neglect of the other joints. When these are examined in succession, those near the most diseased one often present structural changes similar to those in the joint first attacked; whilst the distant

ones are often very difficult to open, because of changes of structure producing cartilaginous, fibrous, calcareous, or bony ankylosis. On tearing open such joints, which often requires great force, the opposed cartilages are seen to be the seat of changes in their cells and hyaline substance, which, with intermixture of the elements of the opposed surfaces, and a change of them into a firmer form of connective tissue, explains why they cohere so firmly.

On such surfaces numerous bloody points are often seen. These are the ends of torn blood-vessels which have been formed in the new tissue into which parts of the cartilage have been converted.

Mr Liston, in the xxiiird vol. of the *Med.-Chirurgical Transactions*, described and gave a drawing of loops of blood-vessels which he had injected, and which he looked upon as indicating the vascularisation of cartilage. After the injection of the vessels of such amputated limbs as those to which I have just referred, I found abundant loopings of blood-vessels in the deeper parts of the cartilages. But instead of such vessels being in contact with the cartilage, they are formed in the midst of medullary matter produced out of the cartilage by proliferation of its cells. The changed action of the non-vascular cartilage has transformed it into a vascular cellular or medullary mass, destined for further changes.

In many parts of such joints the uniting matter of the opposed cartilages is fibro-cartilage, in which, as well as in the deeper parts of the hyaline cartilage, calcification leads to the formation of primary bone, and subsequently to the true laminated bone of bony ankylosis.

Thus it appears that when an altered and healthy nutritive action can be secured in a diseased joint, it is possible that perfect bony ankylosis may happen by indirect transformation of the articular cartilage into bone,—a much more advantageous result than the very rare union of bones deprived altogether of their articular surfaces by the destructive action of disease, and no longer held firmly in contact by the ligaments, which are then too long for their purpose.

The suspension of the increase in length of long bones by ossification at the line of junction of temporary and permanent

cartilage, and the rare ossification of permanent or articular cartilage, suggests the existence of a marked difference in the vital action of these two forms of cartilage, and makes it desirable to have positive evidence that articular cartilage can be transformed into bone.

This can be got by examining eburnated or porcellaneous parts of articular surfaces. I believe it has not been noticed that the free surfaces of such parts are nearly on the original level of the articular cartilage, and that, in general, the level of the other parts of the cartilage, greatly changed in structure, is considerably below that of the porcellaneous parts; indeed, frequently very little of those parts of the cartilage remains on the bone.

Sections of porcellaneous parts show them to be formed of excessively dense bone, such as is never formed where the bone has been preceded by ordinary temporary cartilage. Enclosed in the bony tissue, here and there, are small blocks of easily recognisable articular cartilage, as yet free from ossification, and giving positive evidence that the position of the porcellaneous part was once occupied by articular cartilage. When two surfaces of such newly formed ivory-like bone move on each other, they become highly polished, and often, especially in ginglymoid joints, ground into mutually fitting ridges and grooves. The polish of such surfaces is such as cannot be given by any amount of friction to ordinary bone.

The vital power of temporary and permanent cartilage is widely different, and it is only when the general conditions have become greatly changed that permanent cartilage is transformed into very dense bone, and an ivory-like polish is ever given to the part.

The suggestion that a porcellaneous surface is the result of friction of an articular surface which has been deprived of its cartilage has probably arisen from an imperfect appreciation of the level of such surfaces, in comparison with the original level of the whole articular surface.

Permit me now to direct the attention of the Society for a few moments to the exquisitely adapted anatomical structure of articular surfaces, and to the cause of the terrible suffering which often occurs when these parts become diseased.

The blood-vessels of bone, covered by their porous Haversian layers, end in a series of arches under the cartilage, giving, like the series of arches of a railway viaduct, very great resistance to pressure on the summit of these arches, by a very small amount of material. The intervals of adjacent arches are occupied by nearly solid calcified cartilage, as the intervals of the arches of railway viaducts are filled by ballast; and the surface, now presenting only slight inequalities, is covered by highly elastic articular cartilage, in direct contact with the porous bone only here and there, at the summit of the arches of occasional bony layers.

The bone, largely supplied with blood in its Haversian canals, is freely irrigated throughout with nutritive fluid by its canaliculi;—the cartilage, whether traversed everywhere by lymphatic canals or not, is capable of taking up coloured fluids into all its parts, and is deeply coloured by bile-stained blood-plasma in jaundice, whilst the nearly solid calcified cartilage between the bone and the elastic cartilage, both so completely saturated with nutritive fluid, is only just able to transmit sufficient nutritive fluid through its solid mass to keep it alive. It discharges an admirable mechanical function on the articular surface, but cannot be expected to manifest active nutritive changes.

Let us now follow these tissues when a limb suffers seriously from abnormal nutrition. One or more joints are seriously destroyed, their cartilages are softened, and almost entirely converted into a soft, semi-fluid mass, in which it is difficult to recognise the structure of disintegrating cartilage;—what remains of the articular cartilage tears easily from the bone where this has become transformed into a soft cellular mass; and the synovial membrane has participated in the general disintegrating change.

We look at the other parts of the limb,—needles pass readily into all except the dense parts of the shafts of the bones. On looking into the joints, many of them seem at first sight but little changed; but on looking more carefully, the free surface of the cartilages is seen to have lost much of its substance, and to have become softened, roughened, and thinned, especially near the edges of the surfaces. On inserting one blade of a pair

of forceps under the edge of the thinned cartilage, it tears from the bone with great ease, frequently in a single piece. The bone is softened, and more or less converted into a soft granulation mass, which has broken up in the tearing off of the cartilage.

If it be a lower limb, such cartilages as those on the upper part of the astragalus may be torn off from the lateral and upper articular surfaces in one piece, whilst in some of the smaller joints of the foot various stages of cartilaginous, fibro-cartilaginous, or osseous ankylosis may be observed.

Let us now take one of these detached cartilages between the finger and thumb. Its deep or attached surface is as rough as a piece of sandpaper, for its calcified articular lamella, moulded on the rounded ends of the Haversian systems and their interspaces, has come off from them unchanged, though the bone has lost its lime salts, and has become converted into a soft granulation mass, the superficial surface of the hyaline cartilage having at the same time undergone considerable change, and lost greatly in substance, whilst its continuity with its deep calcified lamella has remained unaffected.

It is plain what has happened. The parts most under the influence of nutrition—the bone and the elastic cartilage—have yielded to the destructive influence of the abnormal nutritive action, whilst the nearly solid calcified cartilage has resisted any change to the last, and retained even its lime salts and its hardness.

What is the effect of this in the living body? In the state of health, the vessels and nerves of the Haversian canals of the bone are preserved from injury by the hard layers of the Haversian systems covering them in, but in the diseased state these layers have become resolved into a soft cellular mass, which allows the sharp edges of the projections on the lower surface of the calcified cartilage to tear both blood-vessels and nerves, and produce small extravasations of blood, and terrible agony from laceration of the nerves.

In these states pressure of the articular surfaces against each other compresses the nerves and vessels, producing but little pain; but when rotation is added to pressure, the spicules of the deep surface of the calcified cartilage are dragged through the nerves and vessels, producing the terrible agony which has

so long been noted as indicating disease of the cartilage and bone, and which occurring repeatedly from spasms of the limb on attempts at sleep, exhaust the sufferer, and compel resort to amputation.

Let us turn now very briefly to the evidence that tissue changes are the results of the vital activity of the tissues themselves; that tissues do their own work, and are not indebted to others outside them; that new forms of tissue are produced in the places where we find them out of the materials previously existing in those parts.

I believe if this be established it will greatly simplify our conceptions of many physiological and pathological processes.

An articular cartilage, previously smooth and compact, often presents irregular cavities, as the result of softening, and molecular disintegration, ulceration, without the aid of any other tissue or visible change in its own deeper parts.

The instances in which it had been supposed that pits on cartilaginous surfaces had been produced by the agency of a new vascular and cellular membrane with nipple-like processes occupying the pits, and easily drawn out of them (figs. 3, 4, 5, 7, 8, 9, 10, 13, 18, 19), were cases of increased proliferation of cartilage cells, with accompanying softening and fibrillation of the hyaline substance, leading to the production of a fibro-cellular layer out of the original tissue, firm enough to be torn off, with its nipple-like processes, from the cartilage, and not unfrequently forming a permanent fibrous cicatrix.

In perfectly healthy cartilages, wounds heal in this way, the uniting fibrous membrane presenting projections, and the cartilage corresponding pits, where enlargement and proliferation of the contents of the original cells form a soft cellular mass, which in its turn becomes a firmly adherent fibrous membrane, with corpuscles on its fibrous bundles (see figs. 17, 18, and 19).

The so-called Howship's lacunæ, and their contained cells, are similar instances on the surface of bones and the fangs of teeth, believed to be in process of absorption. As in many another instance, an exalted action, enlargement, and multiplication of the contents of certain cells has taken place, and these soft masses, lying on the bone yet unsoftened, separate readily

from it during their examination, and leave the hollow cavities called Howship's lacunæ. Their subsequent destination varies in different instances. Because of their frequent presence when bone loses its calcareous matter and its structure changes, they have been said to be agents in absorption of bone; but they are not always present, and are not therefore essential in this process, the greatest amount of bony disintegration taking place in the presence of small succulent cells, possibly the result of a want of cohesion of the elements which elsewhere make up these giant cells.

It is difficult to see the consistency of the view that myeloplaxes, when called osteoclasts, should be regarded as agents in absorbing bone; and on other occasions, when called osteoblasts should be regarded as agents in forming bone.

I am not aware of any one but Mr J. Greig Smith ¹ who has hitherto ventured to suggest doubts whether giant cells are agents connected with the absorption of bone. And I think a careful consideration of the continual production of Haversian spaces to be in their turn converted into new Haversian systems in the normal nutrition of bone, as was suggested and demonstrated by Messrs Tomes and De Morgan, points to entirely different views on the process of absorption. The lime salts may be removed and the structure changed, so as to be no longer recognisable as bone, without the presence of giant cells at all.

During the formation of bone which had been preceded by cartilage and calcified cartilage, there is an almost insensible removal of the parts of the calcified cartilage no longer necessary for support, whilst the cells which constitute the medullary material formed out of the contents of the cartilage cells are engaged in the production of true laminated bone.

This is another instance in which the original tissue transforms itself into different adult tissues by its own vital power, into calcified cartilage, bony layers, blood- and lymph-vessels, nerves and marrow.

Heitzman has well described and figured the transformation of cartilage into medullary cells, and traced the formation of blood corpuscles and blood-vessels at individual parts of the

¹ *Journ. of Anat. and Phys.*, vol. xvi., Jan. 1882.

tissue forming bone from cells which he calls hæmatoblasts; whilst the medullary cells surrounding them are engaged in the formation of the tissue of truly laminated bone. He explains the formation of myeloplaxes as due to the coalescence of medullary corpuscles in a territorial form, and refers to Ziegler's demonstration of their formation by cells migrated between two glass plates as the probable explanation of their occupation of the cavities produced in ivory pegs and dead bone by decalcification and liquefaction.

The appearance of blood-vessels in bone in the early stages of its formation has been usually described as due to intrusions or ingrowths of vascular periosteum or of periosteal vessels, without, I think, any sufficient evidence that such things occur at all. That blood and blood-vessels form out of the cells of medullary matter, the result of development of cartilage cells in spaces more or less closed in by calcified trabeculæ, can, I think, be satisfactorily demonstrated. This method of development is consistent with the mode of development of blood and blood-vessels in the embryo, and adds to the instances showing that tissues are capable of effecting their own changes.

In conclusion, let me submit the following considerations:—

The fibro-nucleated membrane, with its nipple-like processes, which has been supposed to cause ulceration of cartilage, is really formed by a change of the structure of the cartilage itself into cicatricial fibrous connective tissue.

The cells of Howship's lacunæ are the results of the increased development of the corpuscles of the tissue in which we find them, not new structures introduced from without.

Bone enclosed in its case of periosteum and cartilage changes into the cartilage of enchondroma.

Ziegler, in treating of metaplasia, pointed out that cartilage can be transformed into mucoid tissue or areolar tissue; cartilage, into osseous tissue; fibrous tissue, into mucoid tissue and bone; and osseous tissue, into fibrous tissue or cartilage,—one form of connective tissue being changed into another.

Ziegler, Dr Woodhead, and others have abundantly shown that blood- and lymph-vessels are produced by the junction and hollowing out of the branching processes of newly-formed cells,

which are subsequently united with protoplasmic endothelial processes of older vessels to form continuous channels for the circulation of blood.

And I think we cannot but conclude that each individual tissue has power to do its own work in the position which it occupies,—of maintaining its own structure and life,—or of changing itself into another kind of tissue, which may be so different from the original that the transformation is not easy to demonstrate.

DESCRIPTION OF FIGURES, pp. 106–108.

Figs. 1*a* and 2*a*. Softening, swelling, and loosening of the tissue of the free surface of the cartilage of the patella.

Figs. 3 and 4. Great enlargement and change in the contents of the cells, and discharge of their contents.

Fig. 5. Soft nucleated mass produced on the free surface by intermixture of the contents of different cells.

Fig. 6. Calcification of deeply seated cells.

Figs. 7, 8, 9, 10. Formation of fibro-nucleated membrane by the contents of the cells on the superficial surface.

Figs. 11 and 12. Comparison of the healthy perichondrial surface of the costal cartilage of a dog, with the same surface 5 days after a seton had been passed through it.

Fig. 13. Membrane with nipple-like process in costal cartilage of dog.

Fig. 14. First appearance of fibres in hyaline matrix of costal cartilage 40 days after insertion of a seton.

Fig. 15. Effects of actual cautery to femoral trochlea 49 days previously.

Fig. 16. Effects of pressure due to a partial luxation.

Fig. 17. Enlargement of cells and multiplication of their contents near the surfaces of an incision into the cartilage of the patella of a dog 49 days previously.

Figs. 18 and 19. Firm fibrous union by a fibro-nucleated membrane with nipple-like processes after a similar incision to that in Fig. 17, but after the lapse of 24 weeks and 5 days.

Fig. 20. Molecular disintegration—Ulceration.



FIG. 1.

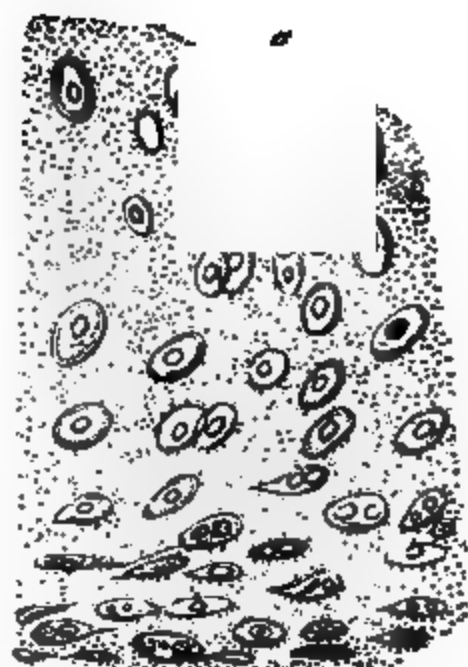


FIG. 2.

FIG. 3.

FIG. 4.

FIG. 5.

FIG. 6.

FIG. 7.

FIG. 8.

FIG. 9.

FIG. 10.

FIG. 13.

FIG. 16.

FIG. 11.

FIG. 12.

FIG. 14.

FIG. 17.

FIG. 18.

FIG. 19.

A MODIFICATION OF THE CHROME SILVER METHOD
FOR NERVE CELLS. By WILLIAM HUNTER, *Pathological
Laboratory, Aberdeen University.*

SINCE the discovery in the year 1875 of Golgi's silver stain, the method has been much worked at and improved upon by many histologists, as Ramón y Cajal, Van Gehuchten, Lenhossék, etc.

The following modification of the process may prove of interest. It is generally supposed that the impregnation can only occur in very small pieces of tissue which have been soaked for at least not more than six weeks in bichromate solution or Müller's fluid. This, however, appears to be an erroneous notion, for I find that completely hardened tissues give good results in most cases (*vide* micro-photographs Nos. 2, 3, 4, 5).

The method I employ is as follows. Instead of soaking small blocks of tissue for several weeks in bichromate solution, thoroughly harden the whole brain and spinal cord in Müller's fluid for a period varying from six weeks to as many months. Small blocks are then taken and dropped directly into a solution of silver nitrate ($\frac{3}{4}$ per cent.). In the majority of cases it will be found that good impregnations have occurred.

This method succeeds best with the brains (especially cerebral cortex) of full-grown animals: foetal tissues, after being hardened, do not give so good results.

Further, by the use of this method the obstacle of hitting the exact point of hardening is got over, and the uncertainty in the production of the desired reaction to a great extent done away with.

In one or two cases the sections have been covered with cover-slips. Although these were mounted at least two months ago, no bad effect has as yet been seen. The preservation of the stain is often a difficult point. Dr Hill,¹ in his recent article on the chrome silver method, states "that when

¹ Hill, *Brain*, 1896, pt. lxxiii. p. 15.

the section is covered with a cover-slip, all the 'staining' may disappear; if the section is mounted in ordinary canada balsam, in four or five hours, although masses of black deposit remain permanently." Some sections prepared about the same time as those mentioned above, according to the osmio-chromate process, and with no cover-slip, are already showing dark yellow masses and granules in the sections, and the cells appear to be losing their colour. It would appear that the reaction obtained with thoroughly hardened tissues is much more permanent than with the rapid osmio-chromate process. The following series of experiments, accompanied by photographs, was conducted on the same lines as Hill¹ followed, viz., to determine the conditions under which the reaction occurs, the limits within which the process may be varied without abolishing the reaction, and to note the effects of these modifications.

Experiment I.—Brain of Cat, put into Müller's fluid immediately after death; left here for seven days, changing the solution once or twice. Pieces about $\frac{1}{4}$ inch in thickness were taken from the motor cortex and put into the following solution—

Potassium Bichromate,	.	.	.	3 grms.
Osmic Acid (1 p.c.),	.	.	.	25 c.c.
Formic Acid,	.	.	.	4 c.c.
Distilled Water,	.	.	.	100 c.c.

Put into warm chamber at 98° Fah. for 5 days: solution changed once: pieces then washed in water for a few minutes, transferred to silver nitrate solution ($\frac{3}{4}$ p.c.) for twenty-four hours in the dark. Silver solution changed once, again washed in water, then embedded in celloidin as follows—

Absolute Alcohol,	.	.	.	1 day.
Absolute Alcohol + Ether,	.	.	.	1 day.
Celloidin Solution,	.	.	.	1 day.

Cut under methylated spirit, clarified, and mounted in dammar lac.

All the layers of the motor cortex could easily be made out. The neuroglia cells of the molecular layer showed their principal process ending in a foot-like enlargement, as described by Schäfer.² The amount of deposit was very little. The experiment was therefore very successful. (*Vide* micro-photograph No. 1.)

Experiment II.—Same Cat's brain as in No. 1, left fourteen days in Müller's fluid. Pieces again taken from motor cortex and of the same thickness—treated exactly as in No. 1.

Scarcely any cells could be made out in any of the sections. The amount of deposit of chromate of silver was much greater than

¹ Hill, *Brain*, 1896, pt. lxxiii. p. 5.

² Schäfer, *Quain's Anatomy*, vol. iii. part i., 1893, p. 167.

usual, not only on the surface of the preparations, but through their substance. The experiment was then unsuccessful.

Experiment III.—Same Cat's brain as before, left for two months in Müller's fluid. The use of the osmio-chromate solution was discarded, owing to the result obtained in No. 2. Pieces were again taken from the cortex, of the same thickness, and put directly out of the Müller's fluid into the silver solution, of the same strength as previously,—left for twenty-four hours in this at the temperature of

FIG. 1.—Adult Cat, Motor Cortex. Brain left seven days in Müller's fluid ; subsequently small blocks left five days in osmio-chromate solution.

98° Fab. The pieces were then embedded in celloidin, this occupying over four days : remaining part of process the same as in No. 1.

The result was quite as good as No. 1. The processes as regards length and delicacy were even better. All varieties of cells could be seen. By cutting fairly thin sections, the amount of deposit was greatly reduced. (*Vide* micro-photograph No. 2.)

Experiment IV.—Same Cat's brain as before, left in Müller's fluid for over three months. Again pieces were taken from the cortex, of the usual thickness, and treated exactly as in No. 3.

The result was as good as in No. 3. Cells of all varieties could be seen, some of them having processes which could be traced right up to the superficial layer of the cortex. Many pyramidal cells had thorns on their protoplasmic processes, which varied in length and usually ended in a small knob—the latter often having a clear central space. These thorns were present in the other experiments also. The amount of deposit was very small. This experiment was therefore very successful.

Experiment V.—Human brain, which had been in Müller's fluid for about five months—pieces $\frac{1}{4}$ inch thick taken from the occipital region

FIG. 2.—Adult Cat, Motor Cortex. Brain left two months in Müller's fluid.

of cortex—unwashed in water—put directly into the silver solution of the same strength as before and for the same length of time—embedded in celloidin—this occupying three or four days, cut and mounted as in No. 1.

The different layers of the occipital cortex were very well marked. The number of pyramidal cells is not so great here as over the motor area. Numerous small cells and granules were to be seen. The precipitate was fair in amount, and mostly deposited around what appeared to be neuroglia cells. The experiment was very successful. (*Vide* micro-photograph No. 3.)

Experiment VI.—Pieces from same brain as in No. 5—from occipital cortex, $\frac{1}{4}$ inch thick—put directly into the silver solution ($\frac{1}{2}$ p.c.) with the addition of one or two drops of formic acid 1-50 solution—remainder of process as in previous experiments.

No trace of any cell could be seen in any of the sections. A very fine granular precipitate was present all through the tissue. The experiment was an absolute failure.

Experiment VII.—Pieces from same brain as in No. 5—from occipital and motor cortex, $\frac{1}{4}$ inch thick, put directly into the osmio-

FIG. 3.—Human Brain, Occipital Cortex. Brain left about five months in Müller's fluid.

chromate solution as used in No. 1 for two nights—washed in water and treated with silver solution, etc., as before.

No trace of any cells to be seen. The very fine granular precipitate as in No. 6 seen here also. The experiment was an absolute failure.

Experiment VIII.—Pieces from same brain and under the same conditions as Nos. 6 and 7. After being two nights in the osmiochromate solution, put directly into the silver solution, having a drop of formic acid solution (as used before): remaining part of process same as before.

This gave an absolutely negative result.

Experiment IX.—Brain from case of Amyotrophic Lateral Sclerosis. Pieces from region of motor area, $\frac{1}{2}$ inch thick—had been over six months in Müller's fluid—no washing in water—pieces put directly into silver solution, and treated subsequently as in former experiments.

The various layers of the motor cortex could be made out. The molecular layer was very indistinct. In the latter were a number of bands (3 to 6), leaving clear spaces between them. These appeared to be composed of deposit. An explanation why these are so regularly laid down cannot be given. They were not present in any of the

FIG. 4.—Human Brain—Case of Amyotrophic Lateral Sclerosis, Motor Cortex. Brain left over six months in Müller's fluid.

previous experiments. Some pyramidal cells had long processes running right up to the molecular layer. Thorns on the processes could also be made out. The amount of deposit scattered through the sections was very small. The experiment was therefore a decided success. (*Vide* micro-photograph No. 4.)

Experiment X.—Human cerebellum which had been for over six months in Müller's fluid—pieces taken from the superior vermis— $\frac{1}{2}$ inch thick—put directly into the silver solution, and treated exactly as in No. 4. The silver solution here used was the old quantity employed for experiment No. 4.

Bergmann's fibres appeared well stained. The granules of the outer

and inner layers well defined. No absolutely complete Purkinje's cells were to be seen, but the branching stems of these could be seen extending into the molecular layer. Very few of the flask-shaped cells themselves could be made out. This may have been due to the plane in which the sections were cut. The amount of deposit was very small. The experiment was successful.

Experiment XI.—Human brain—been in Müller's fluid for about two years—pieces were taken from the motor and occipital cortex, $\frac{1}{4}$ inch thick—treated exactly as in No. 4. The pieces were from eight to ten days in celloidin before being cut.

FIG. 5.—Human Brain, Cerebral Cortex. Brain left about five years in Muller's fluid.

Very few large pyramidal cells to be seen. A very large number of small cells with short processes could be made out. Thorns were present on almost all the processes. The neuroglia cells in some sections were beautifully 'stained.' The deposit was fair in amount. The experiment was successful.

Experiment XII.—Human brain—been about five years in Müller's fluid and well hardened—pieces were taken from the cortex, the same thickness as before, and treated exactly as in Nos. 3 and 4.

A few nerve cells could be seen with delicate branches. The most prominent thing to be noted in the sections was the presence of a very large number of what appeared to be neuroglia cells. These

were much larger than the ones usually found, and their processes extended for very long distances over the field. The processes often looked as if they were connecting cell to cell, but this could not be definitely proved. The deposit was almost absent. The experiment was successful. (*Vide* micro-photograph No. 5.)

From the results of the foregoing experiments and others performed on the same lines, the following may be drawn.

The Material used.—All the experiments were performed on fully developed tissues, mostly from the human subject. The researches of Ramón y Cajal, Gehuchten, Hill, and others have been mostly upon lower animals, and preferably young ones. Cajal uses embryos and very young animals, on the ground that it is the non-medullated, or not yet medullated, fibres that give the reaction. Hill states that it is possible to obtain the reaction through the medullary sheath. The results obtained by the foregoing experiments tend to show that, by the method adopted in them, as good results can be obtained in adult as in young animals.

The Freshness of the Material.—In the experiments, varying periods of time were used, namely, seven days, two months, three months, five months, six months, two to three years, and five years. A satisfactory result was obtained in all of these cases, all giving good reactions. Cajal thinks that by prolonging the hardening in bichromate of potassium some elements may be lost. No proof of this was obtained from the results of the above experiments, thus confirming Hill's view. Many sections cut from blocks of tissue which had been over six months in Müller's fluid showed as beautiful nerve cells as those done by the ordinary Golgi or Cajal method.

The Use of Osmic Acid.—When working with fresh tissues the use of osmic acid is a great advantage. It certainly hastens the hardening, and when the tissue is fresh does not affect the entrance of the silver solution. When working with tissues which have been hardened in Müller's fluid, it is of no use, and even harmful. It is found in the latter case that it so fixes the tissue and completes the hardening that the silver solution cannot penetrate. Osmic acid does not seem to take any part in the reaction.

The Effect of Light.—This does not seem to have any injurious

effect. The reaction can be obtained quite as well in bright sunlight as in total darkness.

The Effect of Warmth.—When using the ordinary Golgi or Cajal method, warmth is not required for the reaction to occur; but when employing hardened tissues, it seems to hasten the reaction, and give a more certain result.

The Silver Salt.—In the experiments given, the *nitrite* was used. The *nitrite* in saturated solution (with the addition of formic acid about 1 to 1000 parts of the solution) gives an excellent result, according to Hill.¹ The addition of a minute quantity of formic acid to the *nitrate* solution always prevented the occurrence of the reaction. The reaction obtained by using the *nitrite* seems to differ considerably from that got by using the *nitrate*.

Embedding in Celloidin.—No occasion for hurrying this process was ever indicated. Most workers on the subject have agreed that the length of time in alcohol should be as short as possible. Cajal obtains the best results from rapidly embedding the blocks in celloidin or paraffin. Lenhossek, Gehrbach, and others never have the blocks of tissue longer than an hour or two in the embedding solutions. Hill has left blocks as long as four days without any perceptible deterioration. Some of the tissues used in the foregoing experiments were left a few days in alcohol and ether, and still gave good results; others were left as long as eight or ten days in celloidin solution before embedding. No bad result was ever got from doing this. By thoroughly embedding the blocks, much finer sections can be obtained, and the celloidin and sections lie much flatter on the slide.

Mounting.—The sections, immediately on being cut, were put into methylated spirit, then into absolute alcohol, clarifying with carbolxylol. Often sections on being clarified were left in the latter reagent for a few days before finally mounting. No bad effect was ever observed from this,—the sections often being much clearer, with the cell processes better marked than before. All the sections were finally mounted in dammar lac.

Briefly stated, my method is as follows:—

The brain and spinal cord are put into Müller's fluid immediately after death, and hardened by the usual method employed

¹ Hill, *Brain*, 1896, pt. lxxiii. p. 14.

for miscellaneous tissues. The hardening period varies from six weeks to five or six months. Small blocks, about $\frac{1}{4}$ inch in thickness, are cut from the desired region, sparingly washed in water, and dropped directly into the silver nitrate solution ($\frac{1}{2}$ per cent.) for twenty-four hours, at a temperature of 98° Fah. This solution is changed once or twice. The pieces are afterwards embedded in celloidin as follows:

Absolute Alcohol,	. . .	1 day.
Absolute Alcohol + Ether,	. . .	1 day.
Celloidin Solution,	. . .	1 day.

Cut the sections under methylated spirit, rapidly dehydrate, clarify with carbolxylol, and mount by the usual method. By the use of the above method it will be found that the reaction can be obtained not only on fresh tissues, but also on hardened ones, and with satisfactory results in the majority of cases.

I must express my indebtedness to Professor Hamilton, in whose laboratory the above experiments were carried out; and also to Drs Dean and Mackintosh for many valuable suggestions.

ON THE ANATOMY OF *MACROPUS EFTS*. By BERTRAM C. A. WINDLE, D.Sc., M.D., M.A. *Professor of Anatomy in Mason College, Birmingham.* and F. G. PARSONS, F.R.C.S., F.L.S., F.Z.S., *Lecturer on Comparative Anatomy at St Thomas's Hospital, London.*

THE following notes are based upon the dissection of two specimens of *Macropus rufus*. The first (A) was a young animal taken from the pouch of its mother: it measured thirteen inches from the tip of its snout to the root of its tail, and the lower incisors were the only teeth projecting beyond the gum. The second specimen (B) was an apparently full-grown animal: as will be seen from the condition of the bones, however, it was not fully matured. As one of us has recently given a full account of the anatomy of *Petrogale xanthopus*,¹ we have used this for purposes of comparison, and have dealt mainly with such points in our present specimens as differ from those already recorded in the other.

OSSEOUS SYSTEM.

In connection with this part of the anatomy, we propose to confine our observations almost entirely to the conditions of the bones dependent upon age, as the osteology of the adult form has been already sufficiently dealt with. *Skull*.—This agrees with the characteristics by which the skull of *Macropus* differs from that of *Petrogale*, except that the infra-orbital canal is double on both sides in A, and on one in B.

When compared with the adult skull, one is struck by the much greater convexity displayed by the more immature form (A) in the roof of the cranium, as also by the shortness of the facial portion, owing to want of antero-posterior growth of the maxilla. The tympanic bone also forms much more of a bulla than it does in the adult, and the tubular part of the bony meatus is not yet developed. The par-occipital and maxillary

¹ Parsons, "On the Anatomy of *Petrogale xanthopus* compared with that of other Kangaroos," *Proc. Zool. Soc.*, 1896, p. 688.

zygomatic processes are quite rudimentary. In all these respects the older specimen (B) conforms to the characters of the adult skull. In (A) the four parts of the *occipital* bone are ununited, in B the basi- and ex-occipitals have fused, but the supra-occipital is still a separate bone. There is in A a distinct *lateral fontanelle* below the posterior inferior angle of the parietal; this has disappeared in B.

The *Atlas* has the whole of the ventral arch in A, between the articular processes, cartilaginous, and the posterior arch has still a thin plate of cartilage in the median line. In B there is a considerable unossified interval in the ventral arch, only a fissure marking the position of the cartilaginous central part of the dorsal. In A the grooves for the sub-occipital nerves are not yet converted into foramina: one of them is completely so in B, whilst the other still presents a fissure between the two parts.

FIG. 1.—Axis of young *Macropus rufus* (B)—dorsal aspect.

The *Axis* in A is composed of four portions: (1) the odontoid; (2) the centrum; (3 and 4) the two sides of the neural arch. Only the dorsal part of the transverse process and vertebral canal is ossified. In B (see fig. 1) the axis consists of the following portions: (1) the lower epiphysial plate; (2) the odontoid, with the anterior articular processes; (3) the centrum and sides of the neural arch, united into one portion of bone; (4) a small diamond-shaped bone intercalated between the odontoid and the anterior part of the centrum, visible both on the ventral and dorsal aspects, which apparently represents the upper epiphysial plate of the centrum.

The other vertebræ have the same centres as the human fœtus presents at birth.

The *Hyoid* bone is interesting in both specimens as presenting elements of the second and third branchial arches in different conditions of development. In the younger specimen the second arch is completely cartilaginous, and is represented by the two cerato-hyals, which are triangular in shape and have their bases applied to one another, whilst their apices are projected outwards and forwards towards the base of the skull. In B these are of the same shape, but the basal portions of both sides are ossified, though the two bones are separate from one another and from the thyro-hyals. These last in A are ossified laterally, and remain cartilaginous near the middle line, whilst in B the ossification is complete, and no traces of cartilage remain in this part of the arch. But in this specimen a bony basihyal exists as in the adult form, and the four other parts of the arch are bound to it by fibrous tissue.

The *Clavicle* has only the diaphysis ossified in A.

The *Scapula* in A has only two centres, one forming the acromion and spine, and the other the rudimentary coracoid. In B a third centre is added between the opposed surfaces of the coracoid nucleus and the glenoid fossa. In A the *Humerus* has no secondary centres, but the supra-condylar foramen is completely ossified, and is wholly formed by the diaphysis. In B there are secondary centres (1) for the two tuberosities (2) for the inferior articular surface, (3) for the external condyle, (4) for the internal. In A both *Radius* and *Ulna* have the shaft ossified, and there is an epiphysis present for the lower ends of the bones, whilst in B there is also an upper epiphysis, which is almost completely united to the diaphysis, the lower being still detached. In the *carpus* of A there are bony centres for the following elements, *scapho-lunar*, *cuneiform*, *pisiform*, *trapezium*, *os magnum*, and *unciform*, but the *trapezoid* has as yet no centre. The metacarpals and phalanges have cartilaginous heads and bases, only the diaphyses being ossified. In B the carpus is fully ossified, each of the metacarpals has a nearly united epiphysis for the head, and each phalanx one in a similar condition for the base. In the *Os innominatum* of A there are centres for ilium, ischium, and pubes, together with one median nucleus for

the sub-pubic bone, and there is no cotyloid bone. In B the three primary parts of the bone are firmly united, and there is a distinct sub-pubic bone. There are also secondary centres for (1) the crest of the ilium, (2) the tuberosity of the ischium, (3) a minute but perfectly distinct centre for the apex of the prominence of bone which projects from the centre of the ileo-pectineal line. The *marsupial bones* do not appear to have been ossified in the younger specimen; in the older one they were fully so.

The *Femur* in A has no upper epiphysis, but in the lower end there are two centres of ossification, one for either condyle. In B the condition of this bone is exactly as has been described in the specimen of *Petrogale*. The groove showing the line of union of the two centres forming the lower end is, however, very evident, and shows that the earlier condition had been the same as that of A.

The *Tibia* in A has two epiphyses at its upper end,—a large one for the greater part of the head, and a smaller one for the anterior part of the same. In B these two epiphyses are almost completely united to one another and to the diaphysis. In both specimens there is an ossified lower epiphysis. The *Fibula* in both has upper and lower epiphyses.

In the *foot* both specimens show the existence of two centres of ossification for the *os calcis*, one for the body and the other for the posterior part of the tuberosity. In the younger specimen one centre of ossification was noticed in each case for the *astragalus*, *cuboid*, *navicular*, and *ecto-cuneiform*, all which are fully ossified in the older individual. In the great fourth toe there are centres for the shaft and head of the metatarsal, and for the shaft and base of the phalanges. In the case of the other three toes in A only the shafts of these bones have any ossific deposit in them, but in B there is also an epiphysis for the head of each metatarsal.

ARTICULAR SYSTEM.

The articular system of *Macropus* closely resembles that of *Petrogale*, so that it will only be necessary to mention the few points in which differences exist. In the *wrist* there is a strong

fibro-cartilaginous band, which passes from the ulnar side of the lower end of the radius to the adjacent part of the cuneiform, which we are inclined to think represents the otherwise absent triangular fibro-cartilage. Again, the peg-like lower end of the ulna is received into a cavity formed partly by the cuneiform and partly by the curiously-shaped pisiform, and not solely by the cuneiform, as in *Petrogale*.

The *knee-joint* presents the following differences:—(1) The *external lateral ligament* consists of two parts, of which the superficial is posterior in position above and anterior below; it is also narrower inferiorly, and attached to the anterior end of the outer aspect of the head of the fibula. The deep part, which is flatter, and placed more anteriorly above, passes under the superficial, to be inserted partly beneath it and partly to the more posterior part of the outer aspect of the head of the fibula. In neither of these parts are the fibres continuous with those of the *Extensor longus digitorum*. (2) The *internal lateral ligament* is very closely attached to the semi-lunar cartilage. (3) The tendon of the *popliteus* contains a very strong fibro-cartilaginous *fabella*, which is placed above the head of the fibula, to which it is attached, and on which it moves freely. It is with this *fabella* that the large *gastrocnemial fabella*, to be more fully described in another section, articulates. (4) The synovial membrane extends a full inch upon the anterior aspect of the femur.

The arrangement of the *external lateral ligament of the ankle-joint*, which differs in some respects from that of *Petrogale*, is as follows. It consists of the following parts:—(1) from the outer malleolus to the outer part of the *os calcis*; (2) from the apex of the malleolus straight down to the prominence on the *os calcis* beneath it: this part can be easily separated into deep and superficial layers; (3) from the outer border of the lower (*i.e.*, articular) aspect of the fibula, passes inward and backward between the articular surfaces of the fibula and of the above-named prominence, to be inserted into the lower edge of the outer aspect of the *astragalus* just below its articular surface; (4) from the inner aspect of the lower end of the fibula, passes between the articular surfaces of that bone and of the *astragalus*, and is inserted into the anterior end of the outer *calcanean* prominence. Thus these two inter-articular ligaments

cross one another inside the joint, one intervening between the corresponding surfaces of the fibula and calcanean prominence, and the other between those of the same bone and the lateral facet of the astragalus.

MUSCULAR SYSTEM.

In this section only those muscles have been mentioned whose arrangement presents some difference from that already recorded for *Petrogale*.

Muscles of the Head and Neck.—The *platysma* is almost aponeurotic in the neck, but considerably thicker and more muscular over the face where it extends on to the masseter covering the facial vein. It is also well developed over the parotid, where it extends to the lower and outer part of the pinna, forming the *depressor auris*. The other muscle of the pinna is at once a *retractor* and *rotator*. It is a strong sheet of muscle, arising from a tendinous intersection between the muscles of opposite sides, which form a V as they pass forwards and outwards to the ear, into the whole of the posterior and mesial aspects of the base of which they are inserted. The *retractor labii superioris* is in two parts: (1) upper and superficial, terminates in a fine tendon, which is inserted into the lip near the angle of the nose; (2) deeper and narrower at its origin, it broadens out as it passes forwards to be inserted into the whole of the remainder of the lip and its angle. The origin of both of these parts is from the lower and anterior border of the orbit. The *sterno-* and *cleido-mastoid* muscles are united, and the 11th nerve pierces the latter. The *Omo-hyoid* is thin and ribbon-like; it has a feeble central tendon in A, but none in B. It is inserted into the junction of the dorsal and middle thirds of the anterior (cephalic) border of the scapula. There is a very large and well-marked *stylo-glossus*, a feeble *stylo-pharyngeus*, and *stylo-hyoid* is fused with digastric in A, separate in B. *Omo-trachelian* arises from the 1, 2, 3 cervical transverse processes, and is inserted into the acromion and adjacent part of the spine of the scapula for about one-fifth of its length. It is covered at its insertion by the *cucullaris*. *Scalenus ventralis* is absent, *s. longus* passes from the 4, 5, 6 cervical transverse processes to the 2 and 3 ribs, *s.*

brevis from the 5, 6, 7 processes to the first rib. There are two *capitis dorsales superficialis et medius*.

Muscles of the Anterior Extremity.—A few fibres of the anterior part of the unsegmented *rhomboid* sheet reach the scapula in B, so that there is a *rhomboides capitis*: in A the muscle belongs only to the neck, though it very nearly reaches the scapula. *Serratus colli* (lev. anguli scapulae) and *serratus ventralis* form a single sheet, which is in A attached to all the cervical vertebrae except the atlas, and to the ribs from the first to the seventh. In B it is attached to all the cervical vertebrae and to the first five ribs. *Infra-spinatus* exceeds *supra-spinatus* in size. *Minor* is a small muscle, quite distinct from *inter-scapularis*, as it is in Petrogale and the Wallaby, though not in the Great Kangaroo. The arrangement of the *pectoral* muscles is substantially the same with in Petrogale, but the *abdomino-pectoralis* is not so well marked as in that species. The *subscapularis* is not supplied by the suprascapular nerve as in Petrogale, but by two branches from the posterior cord, the lower of these also supplying *triceps major*. *Coraco-brachialis brevis* is alone present according to the general rule in Kangaroos, and arises in connection with the coracoid portion of the head of the *humerus longus* axis. *Humeralis*. Macalister found this muscle divided into two slips in *M. ruficollis*, a condition which was not present on either side in the specimens of *rufus*. *Flexor longus cubiti* (*ulnaris*) can easily be divided into a ventral coraco-radial portion, which is fleshy at its origin and tendinous at its insertion, and a dorsal ulno-carpal part, which is tendinous at its origin and fleshy at its insertion. In A both heads of *flexor brevis* (*ulnaris anticus*) are present, as they are in Petrogale: in B we could not find any separation into two parts, though as the muscle was very thick and strong, and arose from a considerable portion of the anterior aspect of the bone as well as from its outer side, it is probable that both were represented, though in a fused condition.

Palmaris longus in B ends in a strong flat tendon, which crosses the anterior annular ligament, and after giving a slip to the pisiform, ends in the fascia of the hand. From the ulnar side of the expansion rise the fibres of the *palmaris brevis*, a large and distinct muscle. From its radial side comes off a

bundle of muscular fibres, which is inserted into the ulnar side of the head of the metacarpal bone of the pollex, and evidently represents the *flexor brevis* of that digit. There is a strong sesamoid cartilage on either side of the hand, that on the ulnar side overlying the pisiform, that on the radial the base of the first metacarpal and the trapezium. The anterior annular ligament stretches between these two cartilages, and from the radial cartilage arises the *abductor pollicis*. In A three *lumbricales* are present, but only two in B, viz., those between the tendons of index and medius, and medius and annularis. *Flexor sublimis digitorum* is a very tiny muscle, which ends in tendons for the four inner digits on both sides in B, whilst in A it is distributed, as in *Petrogale*, to index, medius, and annularis only. As indeed might be expected, the number of tendons belonging to this muscle is clearly variable, since Macalister and Meckel found the same number as existed in our specimen B. The *flexor profundus digitorum* consists of the following parts:—(1) *centralis*, small but quite distinct; (2) *condylo-ulnaris*, the largest head, almost immediately unites with (3) *ulnaris proprius*, which is larger and extends farther up the foramen than (4) *radialis proprius*, which is quite a small muscle. There is no *condylo-radialis*. The above-mentioned portions of the muscle fuse, and form a tendon, which has a remarkable fibro-cartilaginous thickening of an ovoid shape on its ulnar border, where it plays against the pisiform and unciform. The tendon then divides into five stout slips, one for each digit. In the hand there are superficial *adductors* for pollex, index, and minimus, which arise from a common head attached to the carpal bones. *Macropus* therefore wants the adductor annularis which is met with in *Petrogale* and in the Wallaby.

Supinator longus appears to be a variable muscle in the Kangaroos. In *Petrogale* it was inserted into the dorsum of the scaphoid on both sides. Macalister describes it as being inserted into the first metacarpal in the Wallaby, and into the trapezium and first metacarpal in the Great Kangaroo. In our specimen A the insertion of the muscle on both sides is into the lower third of the radius. In B it is on one side inserted into the dorsum of the scaphoid, whilst on the other no trace of the muscle is to be seen. *Extensor carpi radialis longior* is inserted

into the dorsal surface of the metacarpal bone of the index. It is much smaller than the *brevior*, from which it is distinct. According to Macalister, the two muscles are fused and terminate in two tendons, which are inserted into the 2 and 3 metacarpals, a condition which MacCormick believes to be the normal arrangement in the Marsupialia. We are of opinion that a very little pulling will show that in almost every case where these muscles are said to be fused, they will be found to be really separate. *Extensor minimi digiti* sends a slip to annularis in A which we did not see in B.

Muscles of the Posterior Extremity.—*Ilio-tibialis* (sartorius), *tensor fasciæ femoris*, *ecto-gluteus*, and *flexor cruris lateralis* (biceps) form one continuous sheet. *Ecto-gluteus* arises from the posterior sacral and anterior caudal vertebræ: it has no insertion into the femur, but joins a deeper layer from the anterior caudal transverse processes, to form a tendon which is inserted into the outer side of the patella. *Flexor cruris lateralis* arises from the tuber ischii, and very slightly also from the fascia over the caudal muscles: it is inserted into the fascia of the leg, and by its connection with the *ecto-gluteus* also into the patella. It is then continued down as a strong band, which, after uniting with a similar downward prolongation from the *semi-tendinosus*, forms with it a sheath for the posterior surface of the tendo Achillis, upon which it is prolonged downwards as far as the os calcis, where it becomes attached partly to that bone and partly to the sides of the plantaris tendon. There is a *tenuissimus* present. The *gracilis* arises slightly from the base of the marsupial bone, but in other respects it resembles the condition met with in *Petrogale*. *Semi-membranosus* is very closely connected with the adductor mass; in fact, on its superficial aspect, there is no obvious separation between the two until a short distance above the point of their insertion at the knee. A deeper dissection, however, shows that the *ischio-femoralis*, a very well developed muscle, lies between the two, near the femur. The last-named muscle, though closely connected with the adductor mass, associates itself with the hamstring group, by the fact of its obtaining its nerve supply from the large hamstring nerve which comes off from the back of the great sciatic. It is, in fact, apparently a dismemberment

from the deep surface of the semi-membranosus. In specimen A the *gemelli* are arranged in the same manner as in *Petrogale*, but the condition is not quite the same in B, where these muscles are represented by some of the fibres of the *obturator internus*, which arise very close to its point of exit from the pelvis, which cannot be said to constitute a separate muscle. It is probably this condition of affairs which led Meckel to state that the *gemelli* are absent in Kangaroos. *Tibialis anticus* is a very large muscle, which is inserted into the bases of the internal metatarsals, and slightly also into the ento-cuneiform. *Extensor longus digitorum* in A resembled *Petrogale*; in B, as has already been mentioned, it differed from the fact that its tendon was not prolonged up to the femur,—probably only an individual variation. It ends in a single tendon, which forms a wide expansion over the large central toe only. Expansions from this constitute the dorsal parts of the capsules of the metatarso-phalangeal and inter-phalangeal joints. From the deeper surface of this muscle, and very closely connected with it on one side of B, arose a second part, which developed a tendon which passed under that of the long extensor to be inserted into the outer toe. This condition was not met with in A. Only a *peroneus longus* was met with in A; B having a *p. quinti* in addition. The outer head of the *gastrocnemius* possesses a remarkably large fabella, already mentioned as articulating with that of the popliteus. This was crescentic in shape, and in the older specimen measured 2.5 cm. from one cornu to the other. At the upper cornu is a distinct tubercle, from which, as well as from the external condyle above, arises the plantaris, which is thus a double-headed muscle. From the anterior (convex) surface arises the outer head of the *gastrocnemius*, or rather one head of it, for a second comes from the patella. From the inferior cornu arises in B a distinct strong muscle, which joins by its tendon that of the *gastrocnemius* in the lower third of the leg, to constitute the tendo Achillis. This arrangement was not noticed in the younger specimen, which appeared to conform to the condition of *Petrogale*. We think that this third head represents the otherwise absent *soleus*, which may, however, as in B, regain its independence, though taking origin from the large fabella, instead of from the head of the fibula. The *inner*

head of the *gastrocnemius* has also, in the other specimen a fabella, of much smaller size than that of the other head and differently situated. This fabella lies below the origin of the muscle from the back of the condyle of the femur, and between the muscular fibres and that bone, upon which therefore it plays.

The *plantaris*, arising as above mentioned, is a very large muscle, exceeding in size the outer head of the *gastrocnemius*. After being joined by the expansions from the *hamstrings*, its tendon passes over the os calcis into the sole of the foot. There it gives off a slip to form a perforated tendon for the outer toe. The main portion, after this slip has been given off, divides into three parts, of which the two lateral are attached to the spurs on the plantar surface of the large sesamoid plate which underlies the tarso-metatarsal articulation, whilst the central becomes the perforated tendon of the fourth toe. *Popliteus* is very much as in *Petrogale*, but the portion which arises from the semitendinous cartilage is almost completely segmented off from the remainder. There is a very distinct *rotator fibular*.

In the sole of the foot there are three muscles: (1) a thin band on the inner side, which ends in tendons for the 2 and 3 toes: this, which is functionally an *adductor secundus et tertius digitorum*, probably represents the adductor hallucis, which in the absence of that toe, has acquired attachments to those nearest to it; (2) *adductor minimi digiti*, absent in A: (3) *flexor brevis quarti digiti*, much the largest muscle: single at its origin, it divides into two parts at its insertion into the spurs of the sesamoid plate of the metatarso-phalangeal articulation.

VASCULAR SYSTEM.

The heart in A is exactly similar to that of *Petrogale*; and even at the early age of the animal from which it was taken, there are no signs of a fossa ovalis or other foetal structure. In B the condition is similar, except that in the right ventricle there is a very distinct though small moderator band attached just below the ventral musculus papillaris of the valve. From the base of the dorsal musculus several fibrous cords spring, which traverse the cavity; and still nearer the apex there is a

second muscular band, which passes from the dorsal to the ventral wall. The *thymus* in A occupies its usual situation: it consists of two lobes, each of which is about 75 mm. in length. The *aorta* and great vessels are as in *Petrogale*. The *common carotid* bifurcates opposite the cephalic end of the larynx, and at this point the *superior thyroid* is given off, the *lingual* and *facial* arising very shortly afterwards. The *subclavian* and *axillary* arteries are as in *Petrogale*. The *brachial* gives off a small branch some little way above the supra-condylar foramen, which descends to the surface of the forearm, and may correspond to the human *radial*. The remainder of the artery divides into *ulnar* and *posterior interosseous*, as in *Petrogale*. The *abdominal aorta* and its branches are arranged as in *Petrogale*, and the condition of its caudal end, which is that already described by Owen, assumes considerable interest in the light of the observations of Young² on the middle sacral artery. The *aorta* divides into three branches opposite the disk between the fifth and sixth lumbar vertebræ. Of these branches the lateral are the two external iliac arteries, whilst the central, which passes still farther caudalwards, divides into the two *internal iliac* arteries, and gives off the *caudal* artery. It is customary to describe the two internal iliac arteries as branches of the caudal; but assuming, which we believe to be the case, that Young is correct in his view, it would be more accurate to say that in the Kangaroo the external iliac arteries are direct branches of the *aorta*, which subsequently divides into the two internal iliacs and gives off the caudal. The *femoral* artery gives off no definite *external circumflex*, but there is an *internal circumflex*. After giving off the last-named vessel, the femoral divides into *saphenous* and *popliteal*, as in *Petrogale*, and both of these trunks are distributed as in that animal. The veins are arranged as in *Petrogale*, the *vena cava posterior* occupying a position ventral to the iliac arteries.

NERVOUS SYSTEM.

The arrangement of the *cranial nerves* and of the *cervical plexus* is the same as that of *Petrogale*, and there is a *depressor*

¹ "Abnormalities of the middle sacral artery, and their morphological significance," *Jour. of Anat. and Phys.*, vol. xxxi. p. 169.

nerve, which lies close to the vagus. As regards the *brachial plexus*, it has been already mentioned that the subscapularis is not supplied (as it is in *Petrogale*) by the suprascapular nerve. The coraco-brachialis is supplied by a slender twig which comes from the outer cord before the outer head of the median has become detached from it. The *median* itself is formed in the axilla as in man, and not low down in the arm, as in *Petrogale*. It passes through the supracondylar foramen, and in the upper part of the forearm it gives off the *radial*, which goes, as in *Petrogale*, to the dorsal side of the radial three and a half digits. The importance of this method of the origin of the radial nerve, in relation to Paterson's well-known views as to the brachial plexus, has already been alluded to in the paper on *Petrogale*. The rest of the course of the median is as in *Petrogale*. The *ulnar* comes off in the axilla, and gives off in the upper part of the arm a small *internal cutaneous branch*, which supplies the skin over the olecranal region. There is also a *large internal cutaneous*, which is derived from the internal cord. The only point upon which stress need be laid in connection with the lumbar plexus is the high origin of the *internal cutaneous* nerve of the thigh, which can be traced almost entirely into the third lumbar nerve.

DIGESTIVE SYSTEM.

There are eight transverse ridges on the roof of the *hard palate*. The *soft palate* is thick and large, and possesses a long narrow uvula, which appears to contain very little muscular tissue. The *epiglottis* is intranarial. The *tongue* in both specimens possesses three circumvallate papillæ: the fungiform and filiform papillæ are scarcely developed in A, whilst in B they are present in normal numbers. In both, feeble transverse folds indicate the position of the papillæ foliatae, which are better developed than in *Petrogale*. The tongue has no transverse ridges in either specimen. The *salivary glands* correspond in all particulars in B with those of *Petrogale*, but in A there is, in addition to the ordinary glands, a further pair of large size lying at the root of the neck, and meeting one another in the mid-ventral line (see fig. 2). They are pyriform in shape, with

the stalks directed towards the head, and their broader posterior ends overlap the pectoralis major. Histological examination proved that these glands were salivary in their nature, but we did not succeed in tracing the termination of their ducts.

The *stomach* possesses a bifurcated greater cul-de-sac: it has also two very strong longitudinally running muscular bands, one



FIG. 2.—Ventral aspect of neck of fetal *Macropus rufus*. 1, Extra salivary glands. 2, Sublingual glands. 3, Ext. jugular vein. 4, Sterno-hyoid muscle. 5, Mylo-hyoid muscle. 6, Pectoralis.

on either side, which cause the greater curvature to be exceedingly sacculated. The smaller curvature, which measures twelve inches in length in B, as well as that part of the stomach which intervenes between it and the longitudinal bands, is smooth, and devoid of sacculations. A third longitudinal band, running along that part of the lesser curvature which is nearest to the pylorus, causes the formation of an

antrum pylori. There are no glandular patches in the interior of the stomach around the opening of the œsophagus. The *intestines*, like the stomach, closely correspond to the description given of this part of the anatomy of kangaroos by Owen. The cæcum is straight and non-sacculated, and contains several Peyerian patches, some of which are of large size. The *spleen* presents the usual tri-radiate appearance. The *liver* (see fig. 3) consists of right lateral and central, left lateral, spigelian and caudate lobes, and the gall-bladder rests between the two

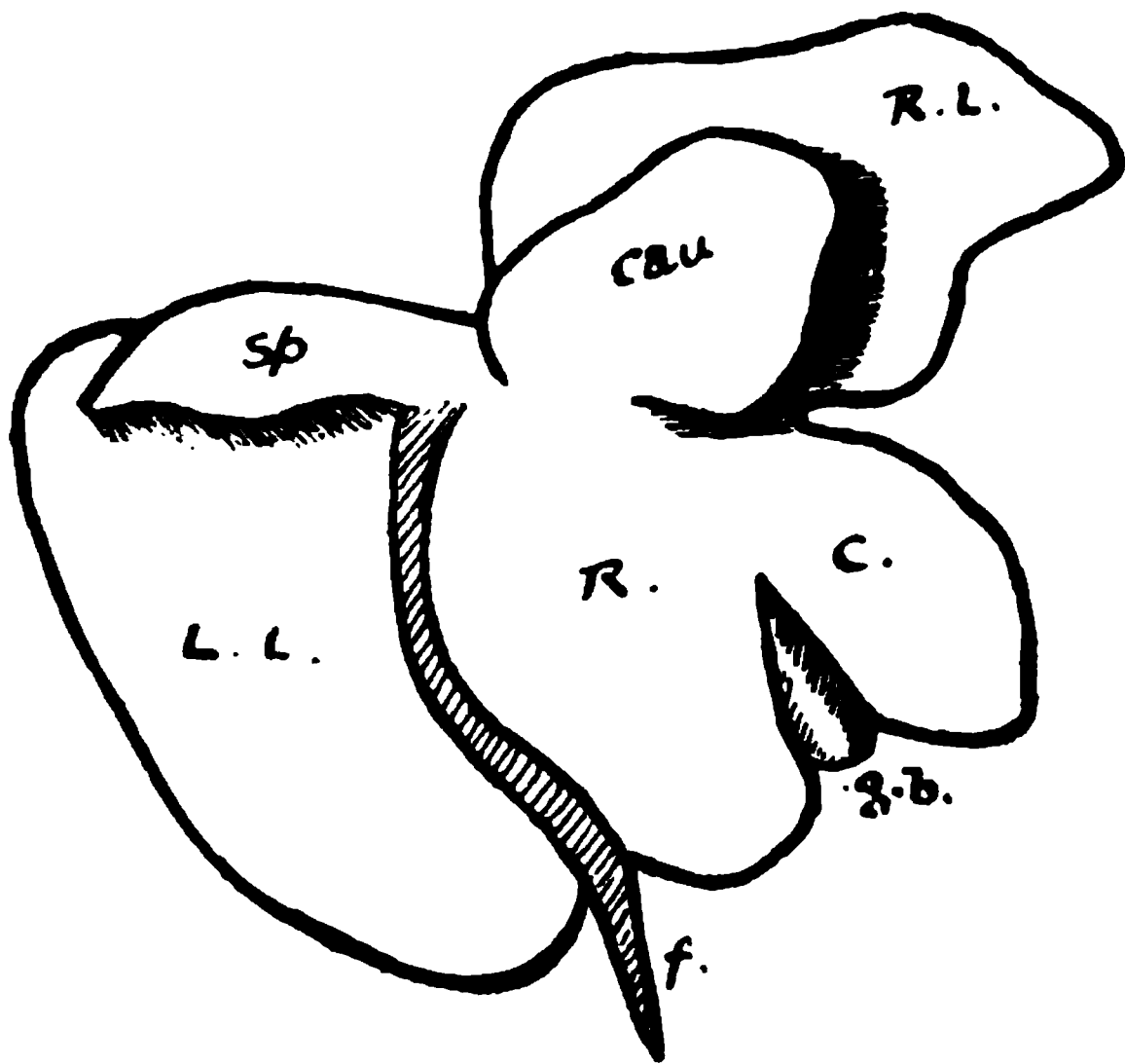


FIG. 3.—Liver of *Macropus rufus*, seen from below. *R.L.*, Right lateral. *R.C.*, Right central. *L.L.*, Left lateral. *Sp*, Spigelian. *Cau*, Caudate lobes. *G.b.*, Gall-bladder. *f.*, Falciform ligament.

portions of the right central. In thus describing the lobulation of the liver, we are aware that we are adopting a different method from that of others who have dealt with the marsupial liver. For these writers the gall-bladder is the line of demarcation between the right and left central lobes. We cannot agree with this method of looking at the matter, since we believe that the falciform ligament, with its contained umbilical vein, is the morphological line of division between the right and left halves of the liver. The gall-bladder is an offshoot from the bile-duct,

and may be absent in some mammals : it ought not, therefore, to be looked upon as having any significance in the division of the liver ; and when it is present, it always rests either upon the right central lobe or between its halves. We regard, in the present instance, that part of the liver which is to the left of the falciform ligament as representing the left central lobe : it is comparatively small, quite destitute of any fissure, and the left lateral lobe must, therefore, be considered as absent. The *kidneys* are nearly on the same level, though the left is slightly anterior in position. In A they show slight transverse depressions, which are not visible in B. These depressions may be indications of lobulation, but no lines of division extend from them into the interior of the organs. The *adrenals* are small flesh-coloured bodies (measuring in A $\frac{1}{4}$ inch antero-posteriorly and $\frac{1}{8}$ inch transversely), which lie a little anterior to the kidneys, but are not connected with them. The older specimen being a female, the internal genitalia were examined. They corresponded to the descriptions given by Owen and by Lister and Fletcher.¹ The last-mentioned authors consider that the central compartment in the Kangaroo is closed in the young form, and becomes open in *Macropus* just before the birth of the foetus. In our specimen the central compartment was closed, and only communicated with the urogenital sinus by the two lateral passages, thus confirming the observation of these writers.

¹ *Proc. Zool. Soc.*, 1881, p. 976.

PRELIMINARY NOTE ON THE STRUCTURE AND FUNCTION OF THE EPIDIDYMIS AND VAS DEFERENS IN THE HIGHER MAMMALIA. By C. F. MYERS-WARD, *Senior Demonstrator of Physiology, Owens College, Manchester.* (PLATE II.)

WHILE the minute structure of the testis has been the object of numerous and extensive researches for many years, the structure and function of the epididymis and vas deferens have received, in comparison, little attention, it being largely taken for granted that these points, for them at any rate, had been already settled.

Text-books of histology and of anatomy, both English and foreign, state that the epithelium of the former is ciliated, that of the latter of the columnar type.

The function of the epididymis is held to be that of a reservoir for the semen, the cilia driving the semen towards the vas deferens, which latter is merely a conducting tube. With the differences in the character of the epithelium in the various sections of the epididymis it is not proposed to deal minutely here.

The structure of the epithelium lining the body of the human epididymis will be first described, and then it will be shown that similar appearances are presented in the epididymis of other animals.

At present, at any rate, it is not to be inferred that strictly corresponding parts have been compared.

The epididymis and vas have been examined in the following animals:—

- | | | |
|------------|----------------|---------|
| 1. Man. | 2. Dog. | 3. Cat. |
| 4. Rabbit. | 5. Guinea-pig. | 6. Rat. |
| | 7. Mouse. | |

In every case, the perfectly fresh organs were fixed and hardened in one or more of the following ways:—

1. Flemming (strong formula, with only $2\frac{1}{2}$ p.c. acetic acid), then alcohol.

2. Marchi's fluid, followed by alcohol.
3. Absolute alcohol.
4. Mercuric chloride (satd. soln. in normal saline), then alcohol.
5. Müller's fluid, and subsequently with alcohol.

The hardened tissues were then nuclear-stained in bulk by Ehrlich's hæmatoxylin, washed out with 30 p.c., 50 p.c., 70 p.c., and 84 p.c. alcohol, strongly counter-stained (*also in bulk*), with 1 p.c. eosin in absolute alcohol, imbedded and cut in paraffin, or after cutting the unstained tissue in paraffin the sections were stained on the slide either with (1) saffranin or (2) Delafield.

In the latter case, the Delafield was washed out in water, passed through increasing strengths of alcohol; finally dehydrated, and at the same time counter-stained with the 1 p.c. eosin in absolute alcohol.

Sections through the body and globus minor of the human epididymis show that the epithelium is composed of at least two, sometimes three kinds of cells (fig. 1).

Bounding the lumen is a layer of cells, of the columnar type.

These may extend outwards as far as the basement membrane (fig. 1, *a*), or may be more or less separated from it by the interposition of the other kind or kinds of cell (fig. 1, *b*, *c*). In some parts there is only one other kind of cell, and that a small angular cell, elongated somewhat in a direction parallel with the circumference of the tubule. Its nucleus is relatively large, usually ovoid, and, like the cell containing it, its long axis is usually circumferentially placed (fig. 1, *b*); in a few cases the long axis is radially placed. The nearer the globus major is approached, the fewer in number are these angular cells, while in the lower part of the globus minor these cells form almost a complete layer surrounding the tubule external to the columnar cells. Where this latter is the case, these cells tend to assume a cubical shape.

Even where this layer does seem complete, it is rare not to find it interrupted at one or more places, to admit the passage outwards of the deep end of one or more of the columnar cells.

In other sections many of the columnar cells do not reach much more than half way towards the basement membrane; and where this is the case, besides the small irregular cells already mentioned, variously shaped cells, whose long axis is generally radial, occupy the space between the deep ends of the columnar

cells and either the basement membrane or the layer of irregular cells.

The columnar cells, which everywhere form a complete layer bounding the cavity, are not very regularly shaped columns (fig 1, *a*).

Where they reach the basement membrane, they vary in length from 35–55 μ , and average 6·3 μ in width at the deep or outer extremity; 5·5 μ at the superficial or inner extremity.

This measurement of the width applies to those cases where the cells line the concave part of the tubule; where they line a convex part, the superficial or inner end of the cell is the wider.

In transverse section these cells are irregularly hexagonal.

To turn, now, to the inner extremities of the cells. The free ends present varied appearances in different, even neighbouring, cells.

Some have the free border produced into *one* long, often 40–50 μ , not very regularly tapering process, which it has hitherto been customary to regard as a huge cilium, under the impression that it is motile (fig. 1, *d*, and *d* in other figs.).

That part of the free border which is not occupied by the process has a highly refractive appearance, and when seen in surface view, as frequently occurs through the tubule being cut obliquely, looks like a cuticular membrane, perforated by holes to allow the passage of the processes. It does not seem possible, however, to separate any such cuticular membrane.

In some cells the tapering pointed flagellum-like structure is replaced by a short, thick, often nearly cylindrical process, with rounded end, directly continuous with the cell protoplasm, of which it is a projection (fig. 1, *e*).

Other cells show each a rather longer finger-shaped process, tapering slightly towards the extremity, which may be slightly or very distinctly clubbed (fig. 1, *f*, *g*).

Still other cells possess each a long, very distinctly tapering process, which, instead of ending in a point, suddenly expands into a large, rounded, pyriform or irregularly-shaped knob (fig. 1, *h*).

Lying in the tube are to be seen rounded, ovoid or irregularly-shaped granular bodies, resembling in all other respects the knobs of the last described form, only they appear to be free (fig. 1, *k*).

Indeed, all the stages can readily be seen, from the condition of a very short, thick, blunt process, not longer than the width of the cell from which it arises, to the flagellum-like pointed process with free knobs in the tubule.

The nuclei of these cells are ovoidal or ellipsoidal, with the long axis radially placed.

Precisely similar appearances are to be found in the epididymis of the Rabbit, Rat, Guinea-pig, and other animals examined; and it is certain that a large percentage of mounted preparations of the epididymis (if they have been carefully prepared) will, even with moderate magnification, 250–350 diams., show in some part most, if not all, the features above described (see figs. 2, 3, 5, 6, 7, 8, 9).

It has been already mentioned that the angular or irregularly cubical cells which lie on the basement membrane increase in number as the tube of the epididymis is traced from the globus major towards the vas deferens.

In the vas deferens itself they form a very well defined layer, which, under low powers, appears to be composed of cubical cells, with relatively large rounded nuclei.

Under higher powers (500 diams. and above) they are seen to be by no means regularly cubical (fig. 13, *a*).

The columnar cells, which form the boundary to the lumen in the vas deferens, resemble, in their general features, the columnar cells of the epididymis; but they are specially characterised by their very elongated, radially placed nuclei (fig. 13, *b*).

The inner extremities of these cells are often prolonged into a flagellum-like process, ending in a point (fig. 13, *c*).

Some cells show the free extremity slightly prolonged into a short clubbed process (fig. 13, *d*). All the vasa deferentia examined showed these processes, but they were specially well seen in the vas deferens of a rat, where practically every columnar cell was provided with a very long pointed process (fig. 12).

It will be seen, therefore, that at one stage at any rate the vas deferens presents an appearance almost exactly identical with that usually described and figured for the epididymis.

The idea suggested itself that perhaps these appearances represented one stage in a cyclical process.

To decide this point if possible, male rats were taken and put

with fresh non-pregnant females every twenty-four hours, killed after varying intervals, and the epididymis and vas then fixed, hardened, stained, cut, and examined (figs. 10, 11).

Up to the present it has not been possible to discover certainly the conditions necessary for obtaining the epididymis in rats with many tubules in the condition described for man, although by chance one gets a specimen exhibiting the process in the most perfect fashion.

Conclusions and Remarks.

1. That at one stage in the life history of the epididymis, appearances very much like budding occur.

2. That the epididymis is almost certainly a secretory tube, the secretion consisting of separated portions of the lining cells, and being destined for the nourishment of the sperm cells.

3. That the vas deferens probably has the same function.

Appearances observed in some cases indicate that the knobs undergo dissolution, forming a granular mass.

Another remarkable feature noticed was that, if the testis showed signs of active spermatogenesis, then few knobs and little sign of budding occurred in the epididymis; while, if the epididymis were loaded with spermatozoa, and the testis (in rats and guinea-pigs) were practically quiescent, then the epididymis exhibited great activity, as judged by abundance of clubs and free knobs.

J. Schaffer¹ has described the appearance of glands in the globus major of the human epididymis. That the appearances he describes are not glands, except in so far as they form part of the epididymis, is certain, for preparations from the human caput epididymis show at one stage ciliated and non-ciliated cells lining the depressions which Schaffer designates glands.

[DESCRIPTION

¹ *Internat. Monats. f. Anat. u. Phys.*, Bd. xiii. Heft 9.

DESCRIPTION OF PLATE II.

Outlines of Cells and Nuclei, drawn by Camera Lucida.

Fig. 1. Portion of epithelium lining body of Human Epididymis. $\times 500$. Zeiss. 2 mm. Apochrom. Compens. Oc. 4.

- a.* Columnar cell reaching basement membrane, in this case with free end produced in short club.
- b.* Basal or irregular cells,—i.e., 2nd kind of cell.
- c.* Intermediate or 3rd kind of cell.
- d.* Cell with pointed flagellum.
- e.* Short club.
- f.* Finger-shaped process.
- g.* Long, well-marked club.
- h.* Knob.
- k.* Free knob.

Fig. 2. From epididymis of rat. $\times 500$. Abs. alc.
Letters as in Fig 1.

Fig. 3. From epididymis of mouse. $\times 500$. Abs. alc.
Letters as in Fig. 1.

As a general rule, only two kinds of cells occur in the epididymis of the mouse, rat, and guinea-pig corresponding to those lettered *a* and *b* in human epididymis.

Fig. 4. View of epithelium in epididymis of guinea-pig. $\times 120$.

Figs. 5, 6, 7, 8, 9. From the same epididymis, showing all the appearances described in man. In fig. 9, *i*, is seen a not infrequent appearance, where the whole knob has not been properly cut off, hence flagellum-like structure, bifid at end. This epididymis showed another point. The spermatozoa which filled the tubule were not separate, but united at the head, the tails being free. A little of this epididymis was teased whilst fresh, and the little groups of united spermatozoa were observed moving about in the fluid. Lettering as Fig. 1.

Fig. 10. Section of epididymis tubule from rat which had been placed with six females, a day with each female. In this case the free knobs (there were none in the section drawn) were especially large and plentiful. $\times 120$.

Fig. 11. Portion of Fig. 10, included by lines 1, 2. $\times 500$.

Fig. 12. Portion of epithelium of vas deferens of rat, showing very well marked flagellum-like processes. $\times 250$.

Fig. 13. From human vas deferens.

- a.* Layer of irregularly cubical cells.
- b.* Characteristic elongated nucleus of columnar cells lining vas.
- c.* Columnar cell, bearing flagellum-like process.
- d.* Very shortly clubbed cell.

Specimens themselves show much more ideally perfect processes than those represented in the figures.

Fig. 2

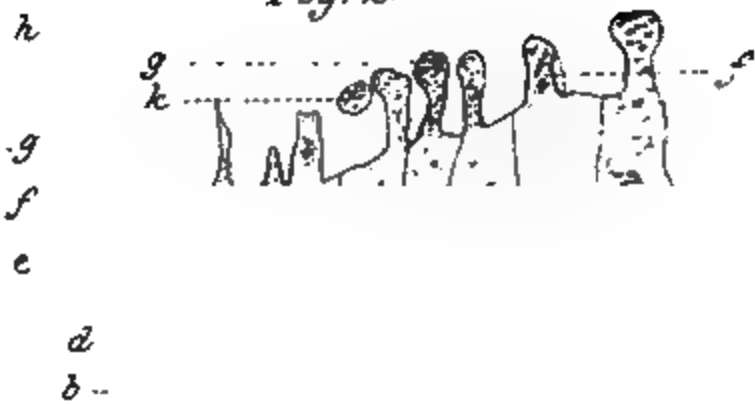


Fig. 6.



Fig. 5.

Fig. 11.

Fig. 3.

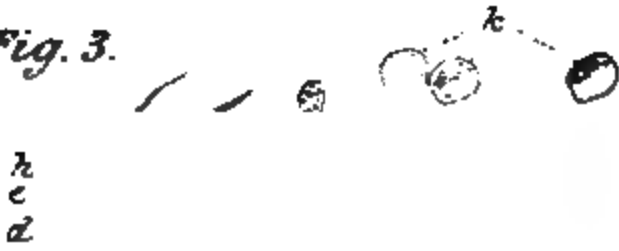


Fig. 4.

g

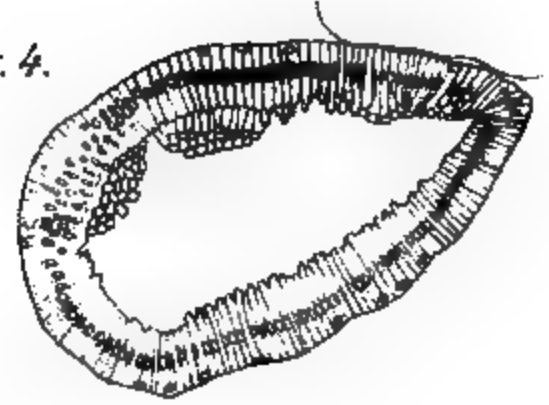


Fig. 8



Fig. 7

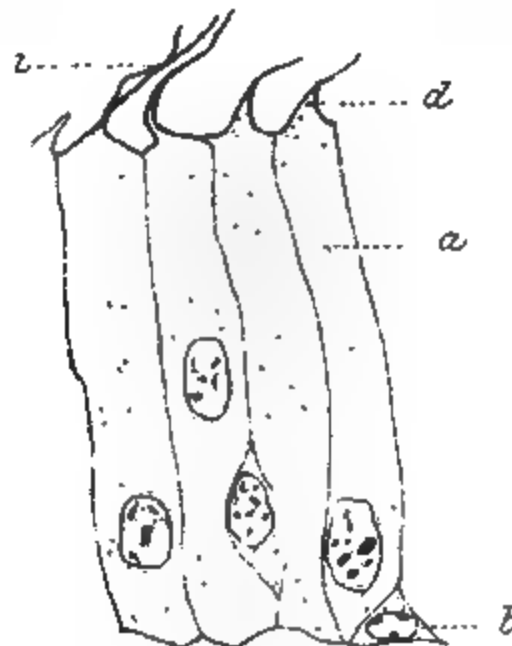


Fig. 10

1

2

Fig. 9.



ON THE STRUCTURE AND MORPHOLOGY OF THE
INTROMITTENT SAC OF THE MALE GUINEA-PIG
(*Cavia cobaya*). By FRANK J. COLE, *Demonstrator of*
Zoology, University College, Liverpool. (PLATE III.)

My attention was first directed to the reproductive organs of the male guinea-pig by Professor Rubert Boyce, who had detected an abnormal condition of the testis in one of the many guinea-pigs used in his laboratory for bacteriological purposes. This abnormality consisted of a very large fatty appendage attached to the anterior end of each testis (see fig. 1, *Cp. E.*)—obviously an hypertrophy of the small adipose appendage normally found in the same position. This appendage extended laterally and internally as a narrow band to unite with the 'cauda' epididymis, and on the left side was found to be $1\frac{3}{4}$ cm. long and $1\frac{1}{2}$ cm. broad. Professor Boyce having very kindly placed the specimen at my disposal, I cut some transverse sections of the appendage, and found that it consisted of a central very vascular core, surrounded by a thick adipose sheath. Coursing through the fat were a few small spermatic tubules, containing undoubted spermatozoa. Seventeen of these tubules were counted in one section. It seems to me, therefore, impossible to escape the conclusion that the appendage normally present in the guinea-pig, and abnormally developed in the specimen under discussion, represents the 'caput' epididymis of other mammals in a degenerate condition. This is assumed by Cannieu (7), who does not, however, seek to prove his point; whilst Prévost and Dumas (1), who were the first to describe the appendage, compare it with the fat bodies of batrachians (p. 172), which is, of course, in harmony with the old view that the corpora adiposa of the frog represent an epididymis. Prévost and Dumas also figure (pl. 11) the hypertrophied condition of the 'caput' epididymis, and assert in the description that this condition is 'often' found in the guinea-pig. This, however, is contrary to the experience of Professor Boyce, who, I believe, has only seen it once. Such a condition is not without normal parallels among the rodentia. In *Dasy-*

procta there are adipose appendages to the epididymis, and they are also characteristic of the rat, whilst Owen (2, p. 76) found them to be very well developed in *Capromys*. It is, further, an interesting fact that in hermaphrodites predominantly male a tendency to fatty degeneration of the epididymis is frequently observed.

This preliminary point having been determined, I started an investigation into the nature of the penial intromittent sac, and arrived at the following, I think, somewhat interesting results:—

Structure.

As is well known in most rodents and marsupials, the penis, in the intervals of sexual activity, is retracted within an eversible fold of skin. Situated below the anal aperture is seen another well-marked aperture, having puckered lips. This is the aperture of the dermal sac formed by the retraction of the penis, and only exists, of course, when the penis is in that condition. If this sac be opened, the penis is seen lying in it with the glans directed backwards (see fig. 2). When the penis is extended, this dermal sac is everted, and forms its outer covering or integument, and is therefore, in a sense, an 'artifact,' whilst the withdrawal of the penis not only forms the sac anew, but involves the curvature of the penis, which, as in most Rodents, is bent on itself.

Dorsal to the aperture of the urethra when the penis is withdrawn, and ventral to it when erected,¹ is seen the large transverse mouth of the intromittent sac (fig. 2, 2). If a ventral incision be made (fig. 3), this sac will be found to be about 1½ cm. long, whilst attached at its base, and lying in its cavity, will be seen two horny styles, having a breadth at their bases of 1 mm. and a length of 5 mm. (fig. 1, 5 and fig. 3, 7). Two dorsal longitudinal folds are also conspicuous (fig. 1, 7 and fig. 3, 3), and these are seen to be the backward prolongations of the lateral lips of the urethral aperture, the ventral lip of the latter consisting of unmodified corpus spongiosum separating the aperture of the

shall use the terms 'dorsal' and 'ventral' to indicate the relations of the sac in the *extended* penis, i.e. when the sac is occupying a ventral position.

urethra from that of the intromittent sac. Attached at the base of the latter, and in the same straight line as the horny styles, are the two retractor 'tendons' of the sac (fig. 1, 4 and fig. 3, 6), which, after a course of about $1\frac{1}{4}$ cm., fan out, and have an elaborate attachment to the integument of the penis. This attachment, though difficult to dissect, and confused by the entrance of small blood-vessels into the 'tendon,' is, however, undoubted, and there is no connection either with the corpus spongiosum or with the corpora cavernosa, whilst there seems also to be a certain quantity of muscle fibre at the attachment.

With regard to the histology of the intromittent sac (see fig. 5), sections show it to have a homogeneous structure throughout. Its lining is thrown into numerous folds and papillæ—all having precisely the same structure as the sac itself. The two erectile styles themselves are simply elongated papillæ, so that the following description applies also to them. Starting from the lining of the cavity of the sac, which is morphologically the outer surface, and ignoring the coagulated mucus, one first encounters a thin layer of superficial horny scales. Underneath this is a well-marked zone of horny fibres of a homogeneous structure, except at the apices of the two horny styles, where the layer somewhat resembles a kind of muco-cartilage, having cavities which sometimes lodge granular cells. The fibres wear away and readily peel off, being recruited from the layer beneath it, and some sections show the horny cells in all stages of transition to horny fibres. Beneath the latter layer is a stratum of cornified cells of some thickness. The most superficial cells are considerably flattened, and have their cell walls somewhat defined, but more centrally the cells seem to become fused together so as to form a horny matrix, in the cavities of which the nuclei are seen lying. The nuclei near the surface are rounded, few in number, and equally scattered; but deeper they are much more numerous and closer together, whilst the most central are columnar, and lie at right angles to the surface. The whole layer finds a close parallel in the cornified epidermis of the frog. Between the cornified cells and the horny fibres traces of a 'stratum granulosum' were seen in parts. So far we have simply been dealing with a modified epidermis, as is obvious from its relations and histology. The dermis itself, which lies underneath it, is so modified and fused

with the corpus spongiosum that it is impossible to distinguish it (fig. 5, 6). The whole layer has the characteristic structure of the corpus spongiosum, with its cavernous or venous spaces, arteries, and trabeculæ, and is histologically indistinguishable from it. Both the intromittent sac and the two horny styles are, therefore, erectile. The styles, being simply papillæ raised on the inner surface of the sac, contain no representative of an outermost layer. A transverse section of one of the horny styles (see fig. 4, 18) shows simply an outer layer of horny fibres, an inner layer of horny cells, and a central core of erectile tissue. With the sac itself this is different, and it is presumed that there must be some membrane forming an outer covering for the corpus spongiosum of the sac (see fig. 4). This, however, my sections fail to demonstrate, unless, as is very likely the case, it be the layer of areolar tissue (fig. 4, 10), which is continued on to the two 'tendons' (see 'Morphology' below).

Turning to the 'tendons' of the intromittent sac, we find that they have an absolutely unique structure (fig. 6). This varies somewhat in different parts, and the following description is based on a section taken at about the middle of a 'tendon.' On the outside there is a fairly thick but extremely loose layer of connective areolar tissue, resembling that covering the intromittent sac itself. The fibres run transversely, and the nuclei are well marked. The greater part of the 'tendon' is necessarily made up of elastic fibres, amongst which are seen a few scattered tendon cells, of the usual stellate character. The fibres of the external areolar sheath pass inwards between the elastic fibres, and appear to unite internally to form a very fine internal areolar lining. From this internal lining there pass a few very fine connective-tissue fibres, which unite with the walls of the artery and vein. The tendon is hollow, and the cavity is almost entirely filled up with a large vein and a small artery, the vein having, of course, thinner walls. The walls of both artery and vein are very simple, those of the vein being very thin, and composed entirely of circular muscle fibres, with well-marked nuclei. The walls of the artery are much thicker, and, from the disposition of the nuclei internally, there seems to be a trace of an endothelial layer. Outside this there is an obvious layer of circular muscle fibres, with large nuclei, whilst, finally, in parts,

there is a distinct connective-tissue layer, connected by fine fibres with the internal areolar lining of the tendon.

Morphology.

There can be no doubt that the intromittent sac of the guinea-pig is a sense organ, and, further, that the sac itself, with its rich nervous supply (see fig. 4, 2), is for experiencing sensation, and the horny styles, without any marked nerve supply, for producing it. When the penis is erected during copulation, the sac is everted; and this is most ingeniously effected by means of the two internal longitudinal folds (see fig. 3, 3). These folds, as will be seen on reference to the fig., are merely the prolongations into the intromittent sac of the lateral boundaries of the urethral aperture, and it will be noticed that their urethral or basal attachments are broad and substantial, whilst that once inside the sac they taper down to a point. Transverse sections show these folds to be highly erectile, in fact much more erectile than the remainder of the intromittent sac; and we can hence readily understand that, when they become erected, there is a tendency, owing to the strong attachment of the base of each fold to the tip of the glans penis, for the intromittent sac to rotate forwards, so as to bring the sac into the same straight line with the rest of the penis, instead of lying underneath and parallel to it. This tendency, however, is prevented—(1) by the integument, and (2) by the two elastic ‘tendons’; and thus the erection of the folds does the only other thing possible for it to do, *i.e.* everts the intromittent sac. When the erection is over, the sac is withdrawn, partly by the elasticity of the two ‘tendons,’ and partly by the muscle fibres in connection with them.

The erection of the intromittent sac is produced by an equally ingenious and interesting apparatus. When, by some chance, I first cut sections through the middle of the tendon, I was much astonished to find that it was hollow, and, further, that this hollowness was due to a large vein and an accompanying small artery (fig. 6). Further investigation showed that these vessels respectively entered and left the ‘tendon’ at the region of its insertion into the integument, and, coursing down its entire length,

supplied and drained the erectile tissue of the sac, the two horny styles, and possibly also the two longitudinal folds above. Here, then, was the mechanism of the erection of the sac. By the contraction of the circular muscles of the vein in the 'tendon' (see above), the cavernous spaces of the erectile tissue of the intromittent sac and its accessories would become gorged with blood received from the artery in the 'tendon,' and would hence become strongly erected. The 'tendons,' therefore, perform a double function: first, they lodge the mechanism for the erection, but *not* the eversion, of the intromittent sac; second, after erection, they withdraw the sac, and serve to keep it in its normal position. I believe the above mechanism is without a parallel in the reproductive apparatus of the Mammalia.

That a tendon should, during its whole length, transmit an artery and vein, was to my mind sufficiently extraordinary to enjoin further investigation. I consequently cut a series of horizontal sections, including both the tendons and the intromittent sac, and found that, as the tendons approached the sac, their structure began to be modified. Instead of consisting of well-marked longitudinal fibres, with comparatively few nuclei, they began to take on the appearance of erectile tissue, the nuclei were more numerous, the fibres began to have a less definite course, cavernous spaces appeared, until finally at the sac itself the structure of the tendon was absolutely indistinguishable from that of the sac. A series of transverse sections through the entire penis shows this difference still more clearly. In these sections the structure of the sac can be compared in the same section with that of the corpus spongiosum urethræ, and it is at once observed, working backwards from the extremity of the penis, that the tendon, at first precisely resembling both the intromittent sac and the corpus spongiosum, gradually changes its structure, until it becomes merged into the elastic fibres shown in fig. 6.

It accordingly follows that these two tendons are simply modified erectile tissue, and this at once explains the presence of the artery and vein. The only morphological difference between the tendon and sac itself, is that in the former there is no representative of the epidermis; but the disappearance of this would be a logical consequence of the posterior portion of the sac taking

on itself the function of tendon, since the horny fibres and horny cells are, of course, non-elastic. I consequently hold that both the tendon and the sac have been derived from the same structure, the anterior part of which became modified to form the sac, and the posterior part to form the tendons. The two horny styles probably appeared later in the phylogenetic history of the apparatus.

A histological examination of the integument of the penis and the wall of the intromittent sac reveals the fact that they are in all respects of essentially similar structure, and it must therefore be concluded that the intromittent sac has been at least partly derived from the integument. Further, the fact that the outer surface of the integument is found to correspond with the lining of the interior of the withdrawn sac (see fig. 4) shows that the latter is formed in much the same way as the central nervous system is—by the fusion of two raised folds. The only difficulty lies in the impossibility of distinguishing between the dermal and the erectile portions of it, since the former is itself erectile, and closely resembles in parts both the corpus spongiosum and the corpora cavernosa (see fig. 4, 8). An account of the development of the sac is a great desideratum; and it seems to me, judging from a knowledge of its adult anatomy, that it must be formed as follows:—The sac would result from the downward growth and ventral fusion of two folds, leaving an aperture anteriorly, which becomes the aperture of the sac, and remaining posteriorly connected with the skin. The corpus spongiosum urethrae must then grow downwards and surround the sac, so as to form its external erectile sheath; whilst posteriorly, by the degeneration of the epidermis and the modification of the dermis and corpus spongiosum, the 'tendons' are formed. This, in brief, is the conclusion to which a lengthened study of this curious apparatus has led me, and the matter must now be left in the hands of those who have the necessary embryological material at their disposal.

LITERATURE.

The first reference to the reproductive organs of the male guinea-pig occurs in a memoir by Prévost and Dumas (1), who

figure the entire genital organs of the male, and in pl. 11, fig. 3, give a very rough figure, but no description, of the everted intromittent sac. Owen (2) next gave a brief description (pp. 75-6), but no figures, of the intromittent sac of the Spotted Cavy (*Cælogenys subfusca*), whilst Rymer-Jones (3) devoted a few lines to the organ in the guinea-pig, and erroneously stated that the muscle fibres of the 'tendon' were derived "from the bulb of the urethra and the rami of the corpora cavernosa." A figure of the extremity of the penis of *Cælogenys* is also given. Owen (4) reproduces Rymer-Jones' figure and description, but states that the 'tendons' are derived from the ischio-cavernosus muscle (i.e., the 'erectores'), this being again an error. The work of Cannieu (7), which I was, unfortunately, unable to procure until the present communication was finished, only anticipates this work in some unimportant respects. He remarks that the two prolongations of the lips of the urethra "aident puissamment au déplissement" of the sac, but his description of the sac is very imperfect, and he erroneously figures the basal row of horny cells (see fig. 5) as forming a perfectly distinct row of separate columnar cells. He points out the resemblance between the origin of the tendons and the outer layer and the sac, and figures them as solid, although he casually remarks in the text that they contain "des vaisseaux qui les parcourent dans toute leur longueur." His fig. 16 is very misleading, and one understands from it that the *whole* of the extremity of the penis is eversible, although fig. 12 contradicts this impression. The eversion of the sac is considered in some way to be assisted by the vessels in the tendons (!), but the resemblance of the outer wall of the sac to the corpus spongiosum is correctly pointed out. Cannieu's figures are very unsatisfactory, his fig. 17, for example, being largely undecipherable. It is further erroneous in two important respects: (1) the folds shown in fig. 4, 17, are lettered as the prolongations of the lips of the urethra, which are *dorsal*, and moreover anterior to the region figured; (2) the wall of the large, lateral, cavernous space in the intromittent sac (see fig. 4) is described as the cellular pouch of the sac.

I have to again express my great indebtedness to Professor G. B. Howes, F.R.S., who very kindly procured for me most of the

literature cited in the Bibliography, and who is ever ready with generous assistance and advice.

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[DESCRIPTION

DESCRIPTION OF PLATE III

Fig. 1. Dissection from the ventral surface of the generative organs of a male guinea-pig. The Cowperian glands are omitted, and the urethral portion of the uterus masculinus is removed. Natural size.

- Bl.* Bladder.
- C. C.* Corpus cavernosum (dissected from urethra, and pinned out).
- C. E.* Cauda epididymis.
- Cp. E.* Fatty abnormal caput epididymis.
- C. S.* Corpus spongiosum.
- G.* Tip of glans penis.
- O. P.* Os penis.
- P.* Penis.
- Pr.* Prostate.
- S.* Scrotal sac (abdominal).
- S. V.* 'Seminal vesicle.'
- T.* Testis.
- U.* Urethra (note its aperture posteriorly at the glans).
- U. M.* Uterus masculinus (hydatid of Morgagni).
- Ur.* Ureters.
- V.* Verumontanum. Aperture of uterus masculinus, and fold of mucous membrane protecting apertures of vasa deferentia and seminal vesicles removed.
- V. D.* Vas deferens.

1. Dots leading to opening of vas deferens into the prostatic urethra at the verumontanum.
2. Dots leading to aperture of seminal vesicle at the side of the verumontanum into the prostatic sinus.
3. Ventral wall of prostatic urethra dissected off to show verumontanum and openings of vasa deferentia and seminal vesicles.
4. Vascular 'tendon' of intromittent sac.
5. Erectile styles of same.
6. Intromittent sac dissected away and laid at side of penis.
7. Prolongations of lip of urethral aperture into the cavity of the intromittent sac.
8. Lip of aperture of intromittent sac.

Fig. 2. Dissection from ventral surface of the withdrawn penis. Outer skin and the fold of skin forming sac for the withdrawn penis removed from the ventral surface. Extremity of penis then turned forward. $\times 2$.

1. Aperture of urethra.
2. Aperture of intromittent sac.
3. Penis turned forward so as to expose its dorsal surface.
4. Outline of penis underneath dermal sac.
5. Point at which penis is bent on itself.

6. Inturned fold of skin, forming sac for withdrawn penis, continued on to glans as its integumentary sheath. Forms external covering of penis when extruded.
7. Outer skin.
8. Aperture of dermal sac (exists only when penis is withdrawn).

Fig. 3. Penis dissected from ventral surface. Skin and ventral wall of intromittent sac removed. $\times 2$.

1. Papilliform tip of glans.
2. Aperture of urethra.
3. Prolongation of lip of urethral aperture into cavity of intromittent sac.
4. Dorsal wall of sac. Its free edge separates the urethral aperture from that of the sac.
5. Cut wall of sac.
6. 'Tendon' of sac.
7. Horny erectile style.
8. Integument seen reflected on to sac, and thence continued as the lining of its interior.

Fig. 4. Transverse section through penis at the region of the bases of the erectile styles. Obj. 3". Drawn with camera, and then reduced to a little less than a half. $\times 15$.

1. Integument. Note outer layer of horny fibres, middle layer of horny cells, and inner layer of the erectile dermis.
2. Nerves in transverse section. Note the others—shown black.
3. Os penis.
4. Periosteum of penial bone.
5. Medullary space (os penis not fully ossified).
6. Corpus cavernosum.
7. Ventral fusion of same.
8. Dotted line, showing where the corpus cavernosum is indistinguishable from the adjacent erectile dermis.
9. Subcutaneous areolar tissue (= portion of albuginea?).
10. Areolar tissue (formed by the separation of the intromittent sac from the adjacent erectile tissue?).
11. Urethra.
12. Corpus spongiosum.
13. Cavernous space.
14. Arteries.
15. Dotted line, showing apposition of intromittent sac and corpus spongiosum.
16. Intromittent sac in transverse section. Note the internal layer of horny fibres, the middle layer of horny cells, and the external coat of erectile tissue. Note also the cavernous spaces and arteries of the latter.
17. Fold of lining of sac. Not one of the prolongations of the lips of the urethra, which are dorsal and situated anterior to this region.
18. Erectile style in transverse section. Note the same layers as in the intromittent sac.

Fig. 5. Longitudinal section through the base of one of the erectile styles (this section will answer for one through the wall of the intromittent sac). Drawn with camera, Leitz 3, Oc. 2. $\times 80$.

1. Mucus.
2. Superficial layer of horny scales.
3. Style continuous with intromittent sac.
4. Layer of longitudinal horny fibres.
5. Layer of cornified cells. Between this and the fibrous layer (4) traces of a 'stratum granulosum' are sometimes seen.
6. Central core of cavernous erectile tissue.
7. Arteries of same.
8. Venous or cavernous spaces of same.

Fig. 6. Transverse section of one of the tendons of the intromittent sac, showing the erectile apparatus of the sac. Drawn with camera, Leitz 3, Oc. 2. $\times 80$.

1. External sheath of areolar tissue. Fibres transverse.
2. Tendon fibres in transverse section. Note the few scattered stellate tendon cells.
3. Very faint internal lining of areolar tissue. Fibres transverse.
4. Scattered connective-tissue fibres uniting the internal areolar lining with the artery and vein.
5. Erectile vein.
6. Erectile artery.
7. Outer connective-tissue coat of artery.

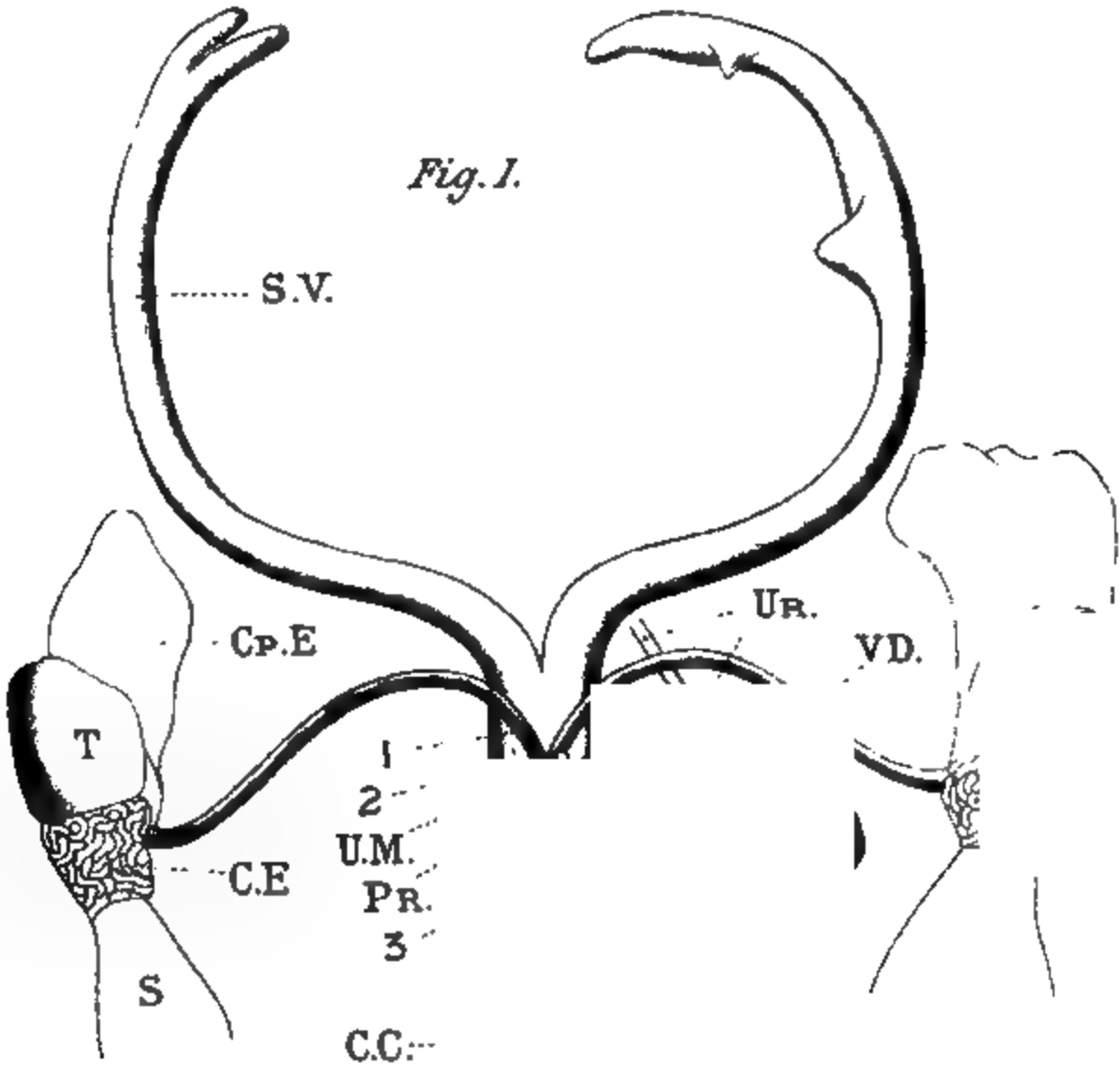


Fig.

Fig. 3.

1
8
7

4
5
6
4
5
6



U
P
O.P.
G.

4
2
1

Fig. 5.

3 5 6

8

Fig. 6.

Fig. 6.

2

1

2

8

Fig. 4.

15 4 5

7

13

14

18

2

ENDARTERITIS PROLIFERENS. By W. AINSLIE HOLLIS,
M.D. Cantab., F.R.C.P. Lond., *Senior Physician to the
Sussex County Hospital.*

Pathogenesis.—Endarteritis proliferens vel obliterans is essentially a disease of the smaller vessels; and it so far differs from atheroma, which attacks by preference the aorta and the large central arteries. Besides this difference in the distribution of the two diseases, their incidence locally and their subsequent evolution are dissimilar. These peculiarities have led some pathologists to assume—wrongly, I believe, although perhaps not unnaturally—that their etiology must necessarily be unlike. In a series of papers published elsewhere,¹ I have adduced reasons for the belief that in many instances atheroma is due to the occasional presence of obnoxious foreign particles in the blood stream. Whether these small particles are in every case the true etiological factors of atheroma is likely to remain a debatable question for some time to come. Meanwhile, the provisional acceptance of such an hypothesis appears more reasonable to my mind than to assume a knowledge of its causation by vaguely ascribing atheroma to senility, mental worry, or overwork, as is now too often done.

On the other hand, the etiology of endarteritis proliferens does not present quite the same difficulty that atheroma does, because pathologists are in a general accord when they describe this disease as one “brought about, as a rule, by some general irritant, which affects the arteries, along with the connective tissue of the organ generally.”² Here, however, my interpretation of the word ‘irritant’ may differ considerably from that of the authors quoted. From the examples of this disease which have come under my notice, and to which special reference will be made in this paper, the association of atheroma

¹ *Journ. Path. and Bacteriol.*, London, vol. 3, pp. 1 *et seq.* *Tr. Royal Med. Chir. Soc.*, vol. lxxvii. p. 69.

² *Ibid.*, vol. iv. p. 83. Paper by Drs Coats and Auld.

with endarteritis proliferens is far from unusual. The two cases from which the photographs were taken to illustrate these remarks were both of them affected with extensive aortic atheroma.

In cases of advanced atheroma, the blood must repeatedly convey, besides its proper corpuscular elements, the granular detritus washed from the surface of a crumbling patch of intima. Whatever may be the ultimate destination of these particles matters not as regards our present inquiry. It is evident that many, if not all, of them will strike against the walls of the vessels through which they pass; and, other things being equal, the smaller the artery, the more frequently will such accidents probably happen. The repeated impact of foreign material against the living walls of a small artery will, I assume, mainly produce two results,—first: an immediate reaction of the endothelium, subjected to the blows. What this reaction consists in remains at present unknown. Possibly it may take the form of active molecular changes in the affected cells, to which the words ‘stimulation’ or ‘irritation’ may be applicable. Subsequently, and as a consequence of this irritation, secondary effects will arise, the chief one of which is probably a spasmodic contraction of the muscular coat. Now, I wish to show in the following pages that the histology of endarteritis proliferens singles out these two structures, the endothelium and the contractile media, as specially affected in this disease. All the evidence, then, at my disposal points to the presence of foreign particles in the blood as an important factor in the causation of endarteritis proliferens, whatever else may occasionally induce it.

Histology.—The sections described in this paper were prepared in a similar manner: they were first hardened in a 10 per cent. solution of formalin; then stained, and finally mounted in canada balsam. Although text-books have repeatedly described and illustrated, oftentimes diagrammatically, the transverse section of healthy artery, perhaps I may be permitted to give a photograph of the intima of a popliteal artery from a 6–7 months foetus which died *in utero*, and was removed at its mother’s autopsy. It is important to compare the inner surface of an artery absolutely free from the suspicion of contamination

through the circulation with others which have been admittedly exposed to contamination. I shall not tire the readers of the *Journal* with a description of the figure. It speaks for itself. (See fig. 1.) I shall, however, refer to it hereafter.

The next illustration (fig. 2) represents a transverse section of an upper oesophageal branch of the aorta from a woman aged 69 years, who died of cancer, involving the cardiac end of the stomach. The portion shown in the figure was situated a few millimetres only from a very atheromatous aorta. There is no doubt about the extent or nature of the disease affecting the arterial coats in this figure. We can see the lumen of the

FIG. 1.—Transverse section of popliteal artery, foetus 6 months. The intima only is shown. Zeiss F. $\times 582.9$.

vessel is much diminished by endothelial cell proliferation, occurring mostly in the shape of rounded projections. These are separated from one another by deep indentations, which appear to extend almost to the muscular coat, and probably represent the longitudinal furrows, into which the intima is thrown by the contraction of its muscular ring. As, however, it will be more convenient to consider the histology of this disease with regard especially to the early stages of its growth and development, I pass on to the next illustration (fig. 3). This also depicts a cross-section of an oesophageal branch of the aorta.

The specimen was taken at the autopsy of a man aged 61 years. He suffered from dysphagia for six months before death. At the post-mortem examination a stricture of the cesophagus was found, commencing about an inch above the level of the bifurcation of the trachea, and extending for two inches downwards. The tissues were greatly thickened around the stricture; and opposite the bifurcation there was an opening into the left bronchus, the size of a sixpence, surrounded by fungating, ulcerous walls. The glands adjacent the stricture

FIG. 2.—Transverse section cesophageal branch of aorta, with advanced endarteritis proliferans, from a case of cancer of stomach cardia. Zeiss DD. $\times 144.4$.

were infiltrated with a soft yellowish-white material. The aorta was very atheromatous.

The endarteritis in this instance has not led to such an excessive proliferation of endothelium as was observable in the previous figure. There is, however, an overgrowth, consisting for the most part of small, ill-developed cells. A sort of leveling up process has then apparently commenced. The longitudinal folds into which the intima of a small artery is naturally

thrown by the contraction of its muscular coat were first filled and subsequently obliterated by the young cell formation. This is well shown in figure 4, where we can trace the original boundary-line of the renal arteriole as it apparently dives into the new tissues. The nuclei were unfortunately not stained in this section. We can, however, observe them in figure 3. Their arrangement is peculiar. Whilst those in the inner lining of the vessel are fortuitously dotted through the new

FIG. 2a.—Transverse section of an oesophageal branch of aorta. Case of carcinoma of cardiac end of stomach. Zeiss B.

tissues, a large number of the spindle-shaped nuclei in the outer endothelial layers are arranged with their long axes radially. From one or the other pole of the nuclear body we may, not rarely, see thread-like extensions, which pass oftentimes between two adjacent cells. In the inner and more irregularly shaped cells I have occasionally found two nuclear prolongations from one corpuscle. These highly stained filaments, I presume, are merely pseudopodial extensions of the nuclear plasma. If this

interpretation of their function is a true one, it follows that we have here to deal with little masses of protoplasm, formerly endowed with independent powers of locomotion. To some writers who doubt the presence of vagrant corpuscles among the arterial tissues, except as rare, and hence uninteresting, strangers, this suggestion will not be acceptable; yet the existence of 'free nuclei' in such situations is admitted by many pathologists. If we grant these independent bodies the power of locomotion

FIG. 8.—Transverse section of an oesophageal branch of an atheromatous aorta. Early stage of endarteritis proliferans. From a photograph. Zeiss F. $\times 490$.

during life, their arrangement in the arterial walls, as above described, gains in significance what it loses in singularity. We can then account for their dissimilarity in the inner and the outer layers of the endothelium. The newly formed cellular lining of the vessel, less cohesive than the older basement cells, permits freer movements among nuclear bodies embedded within it; hence their spheroidal or broadly pyriform shapes when compared with the slender spindle-like corpuscles of the deeper layers, for the latter are laterally compressed in their

passage through the firmer and more resistant tissues of the original arterial wall.

According to my observations, then, it would appear that endarteritis proliferens affects an artery somewhat in the following manner. By the repeated impact of foreign particles against the sides of a small artery a state of 'irritation,' or 'molecular unrest,' as I prefer to call the condition, is established within certain endothelial cells. This unrest manifests itself physiologically by, as it were, rousing the little central mass of nuclear plasm of the cell from its dormant condition to one of active movements. The nuclear disturbance is quickly made known to the vasomotor nerves, and contraction of the artery follows. Now, as we shall see more completely when I come to consider the formation of the tubular clot, this spasmodic contraction of the muscular coat of the vessel is, under such circumstances, about the worst misfortune that could happen. By occurring, as it probably does, during the passage of a cloud of noxious particles through the artery, it enhances the risk that is always present of some being retained within the folds of the intima, to form a still more permanent source of irritation. Hence it happens that the cells at the bottom of a longitudinal fold are more liable to disturbance from this cause than others situated elsewhere. Moreover, from the physical laxness of the tissues in the same situation migrating leucocytes will probably select the furrows as points of departure, a further source of 'molecular unrest' to the neighbouring endothelium.

The existence of free nuclei in the walls of a blood-vessel almost suggests the presence of denucleated cells there. That such cells occur amidst the endothelium of a normal artery I feel confident; the more so, as their presence seems to have been tacitly admitted by some of the leading histologists and pathologists of the present day. I have before me at the time of writing two text-books, selected at random, one upon human histology, the other on practical pathology, each by well-known men. A cross-section of a normal artery forms one of the many beautiful figures with which each work is embellished. The lumen of the vessel, as drawn, is margined in either case by a series of dotted projections, alternating with others which are undotted. The text of each work informs the reader that the

dotted projections represent nucleated endothelium. What the undotted spaces depict is not stated, although in one figure about 50 p.c. of the margin, and in the other fully a fourth, is so drawn. I assume that the artists intended to show by the blank spaces their inability to see any nuclei at those parts. I do not wish to assert that one cell in every four, lining a normal artery, is without a visible nucleus, even in well stained sections, but I maintain that a considerable percentage of endothelial cells are normally without stained nuclei when seen as microscopic preparations (fig. 1). Now, the absence of a visible nucleus may theoretically, I take it, be due to three causes:—(1) It may not take the selected stain. In such cases, however, the outline of the nucleus is always faintly perceptible, if the light is rightly arranged. (2) The cell may never have had a nucleus,—a suggestion of little value. (3) Finally, the nucleus may have escaped from the cell, and consequently the latter was actually denucleated at the time the section was made. The last explanation, in so far as it also seems specially applicable to the new cell formation of endarteritis proliferens, I shall here adopt as the true one.

To resume the progressive history of this disease. When, through over-stimulation, the potential energy of a celled nucleus is converted into active movement, it may lead to the subdivision of the nucleus and the formation of daughter cells on the inner surface of the artery; or a part or the whole of the nucleus may escape through the cell-wall, producing two results, a free nucleus and a denucleated cell. When, by some such process, the natural folds of the intima have been locally obliterated, and the dilation of the artery consequently restricted (figs. 3 and 4), an interesting pathological cycle is apparently induced. As I have elsewhere stated, although we cannot follow the actual movements of a locomotory corpuscle in a stained and mounted section, we may frequently infer the direction in which it was travelling at the time of death from two considerations; namely, that it would probably protrude its pseudopod towards the point it was making; or, secondly, that the vacant burrow it had already made whilst passing through the resistant tissues would be behind it. Viewing their probable movements in this light, I have come to the conclusion, as the

result of many observations, that the little roving protoplasmic masses mainly pass in two directions through the diseased tissues. Whilst a certain number of them apparently force their way outwards between the cells of old endothelium at the bottom of the filled-in furrows, others, starting from the areolar bed, which separates the intima and the media, move inwards, passing, for the most part, through the alternate folds of endothelium dividing the furrows (fig. 3). In cross-sections

FIG. 4.—Transverse section of a renal arteriole, in a case of kidney infarct, showing endarteritis proliferens in early stage. From a case of cancer of the head of pancreas. A photograph. Zeiss F. $\times 600$.

the apices of these folds are often visibly frayed out, their brush-like tops pointing inwards towards the blood current. This brush-like top is, I consider, due first to the escape of the nucleus from an apical cell into the newly formed tissue beyond; secondly, to the subsequent passage of inward bound motile corpuscles along the same route.¹ Functionally, the frayed

¹ In connection with this subject, compare the observations of M. L. Ranvier on the physiological role of leucocytes in corneal wounds, the formation of 'synaptic' fibres, and the proliferation of the epithelium. (*Sem. Med.*, March 12, 1897.)

out apex is of importance, as it evidently assists in holding together the feebly cohesive tissues then lining the artery. By such means are the new tissues in endarteritis proliferans welded, as it were, to the old. In the earlier stages of the disease, only here and there can a disrupted fold be seen; when it is advanced, few, if any, of the folds remain intact (fig. 5).

FIG. 5.—Transverse section of an oesophageal aortic branch showing extensive proliferation of the endothelium. Case 2. From a photograph. Zeiss F. $\times 900$.

This change is in accordance with the progressive nature of the disease.

In offering this interpretation of the chief facts observed by me in the etiology and development of this disease, I do so without prejudice to the many excellent papers already published on this subject. I may perhaps be permitted to state that, in giving again prominence to the acts and wanderings of the locomotory corpuscle, I have in mind the history of a little speck of living protoplasm, endowed with the power of *slowly* forcing a passage through the surrounding tissues, but the direction and the speed of whose movements are mainly deter-

Also a paper by Miss Lily Huie on the changes which take place in the protoplasm and nucleus of the gland cells in the tentacles of the sun-dew, *Drosera rotundifolia*, after the feeding the leaf with pieces of white of egg. The conclusion is drawn, that changes indicative of great activity of the nuclear organs are not exclusively characteristic of cell-division. (*Quart. Jour. Micr. Sc.*, Jan. 1897.)

mined by the physical needs of the living tissues in which it is buried, and of which even itself forms an integral part.

DESCRIPTION OF THE FIGURES, pp. 155-162;

WITH APPROXIMATE MAGNIFICATION.

Fig. 1. Transverse section of the popliteal artery of a 6-7 mon. foetus. The intima only is shown. From a photograph. $\times 532$.

Fig. 2. Transverse section of an œsophageal branch of an atheromatous aorta, showing advanced endarteritis proliferens. From a photograph. $\times 150$. — Fig. 2B. Another section of the same.

Fig. 3. Transverse section of an œsophageal branch of an atheromatous aorta. Early stage of endarteritis proliferens. From a photograph. $\times 490$.

Fig. 4. Transverse section of a renal arteriole, showing endarteritis proliferens in early stage. From a case of cancer of the head of pancreas. A photograph. $\times 600$.

Fig. 5. Transverse section of an œsophageal aortic branch, showing extensive proliferation of the endothelium. Case 2. From a photograph. $\times 900$.

SEVENTH REPORT OF THE COMMITTEE OF COLLECTIVE INVESTIGATION OF THE ANATOMICAL SOCIETY OF GREAT BRITAIN AND IRELAND, FOR THE YEAR 1896-97.¹ Reported by F. G. PARSONS and ARTHUR KEITH.

THE following questions were issued by the Committee of Collective Investigation of the Anatomical Society early in October 1896:—

1. The frequency of an opening between the right and left auricles at the seat of the foetal foramen ovale. The number of cases in which the opening is looked for should be noted, and the sex and age of each recorded. In those cases where a patency exists, an outline drawing should be sent in, and the size of the opening determined.

2. The arrangement and number of the lymphatic glands accompanying the common, external, and internal iliac arteries. If possible, both sides of each body should be examined, and the age, sex, and any special cause of death recorded. As there is reason to believe that age affects the glands considerably, any observations on children and young adults in the post-mortem room will be specially welcome. In their report for 1895-96 the Committee have published a figure showing provisionally the arrangement of these glands, and they beg to recommend that all returns should be accompanied by similar diagrams.

3. The position of the spinal accessory nerve? Whether it passes outward between the jugular vein and internal carotid artery, or between the jugular vein and the atlas? Whether it perforates the sterno-mastoid or not: if so, does the whole nerve perforate, or only a part? Which division of the sterno-mastoid does it perforate?

4. The presence of sesamoid bodies in either head of the

¹ The Sixth Report will be found on p. 31 of the *Journal of Anatomy*, vol. xxx.

gastrocnemius and in the tendon of the peroneus longus. If possible, the nature of these bodies (fibrous, fibro-cartilaginous, cartilaginous, or osseous) should be stated.

The Committee is pleased to notice a great improvement on the returns of last year. It ventures to hope, however, that many of the large institutions which have not responded to the appeal on this occasion will do so on the next. It should be borne in mind by gentlemen sending in reports that the Committee will be pleased to receive, at the same time, suggestions for future research.

QUESTION I.

The frequency of an opening between the right and left auricles at the seat of the foetal foramen ovale.

Returns in answer to this question have been received from the following:—

Dr A. Low, Aberdeen University; Mr E. Parkes, Dublin University; Dr Haygarth, Edinburgh University; Dr Madge Maclean, Queen Margaret's College, Glasgow; Dr Smyth, Queen's College, Belfast; Mr Prentice, University College, Liverpool; Dr Sequeira, London Hospital; Dr Voelker, Middlesex Hospital; Mr Acland, St Thomas's Hospital; Dr Marett Tims and Mr Dawson, Westminster Hospital.

The most complete return is that by Dr Sequeira of the London Hospital. As he has gone into more details than were asked in the question, we shall first record his conclusions separately, and then use his statistics, together with those received from other sources:—

A series of Observations upon 188 human hearts, by J. H. Sequeira, M.D., M.R.C.P., Medical Registrar to the London Hospital, Physician to the North-Eastern Hospital for Children.

The observations here recorded were made by the kind permission of the pathologists in the post-mortem room of the London Hospital. Two hundred hearts were examined. They were as nearly consecutive as the exigencies of pathological demonstrations and the calls upon my time permitted. Owing to incomplete notes, I have had to exclude 12 specimens; and, as time presses, I am sending statistics of 188 cases.

The points I have noted are—

1. The presence or absence of the foramen ovale.
2. Its size and character when present.
3. The condition of the fossa ovalis and annulus.
4. The condition of the Eustachian valve.

5. The presence of endocardial bands in the cavities of the heart.
6. The condition of the valves, especially the aortic and pulmonary.

1. *Foramen ovale.*

There were 61 patencies in 188 cases = 32.4 p.c.
Of these there were 36 „ „ 108 males = 33.3 p.c.
Of these there were 25 „ „ 80 females = 31.25 p.c.

TABLE.

				MALES.		FEMALES.	
Age.				Cases.	Patent.	Cases.	Patent.
Under 1 year				2	2	4	4
Over 1 and under 5				10	6	6	4
„ 5 „ „ 10				7	1	2	1
„ 10 „ „ 20				12	3	6	1
„ 20 „ „ 30				11	4	14	4
„ 30 „ „ 40				19	3	16	3
„ 40 „ „ 50				18	8	16	3
„ 50 „ „ 60				13	4	11	1
„ 60 „ „ 70				13	4	5	4
„ 70				3	1	—	—
				108	36	80	25

2a. *Size of patency.*—Where practicable this was measured by means of a graduated cone. Where the patency was funnel-shaped the size of the outer orifice is given below.

SIZE.				CASES.
Minute, admitting the head of a fine probe				8
2 millimetres diameter				7
2.5 „ „				11
3 „ „				3
4 „ „				2
5 „ „				16
6 „ „				4
7 „ „				1
8 „ „				8
1 centimetre „				1
				61

2b. *Form of patency.*—The most common form is an oblique slit, under the annulus on the right side, and under a fold of endocardium on the left. The obliquity of the slit is such that the opening is not competent to allow the passage of blood, especially when the auricles contract.

Diagrammatic section.—In only two cases was it possible for a leakage to have taken place. In some cases the slit on the left side simulates the orifice of a vein. In a few cases (7 out of 61) the opening was funnel-shaped, the outer orifice being on the right side. One funnel was 2 centimetres long, and ran very obliquely. In the thin septum in one case (where there was also a large oblique patency), there were several minute holes.

In a large number of cases there is a blind slit under the annulus, in the position of the slit-like patency. In one instance this was 2 centimetres long, and in another 1·8 centimetre. A similar condition

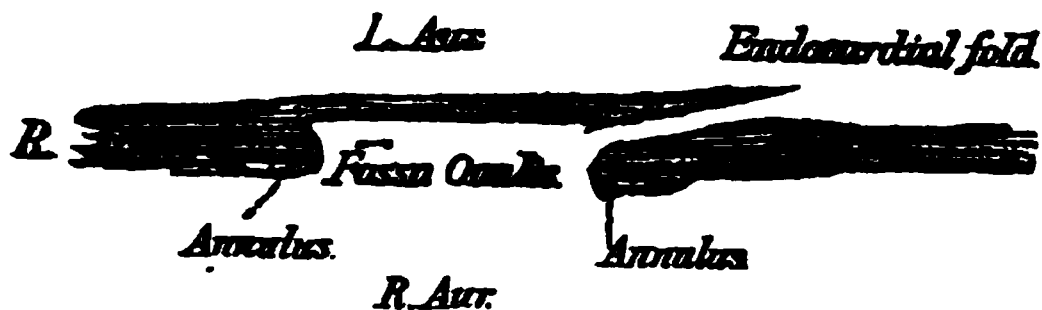


FIG. 1.—Diagrammatic section through a perforate Fossa Ovalis.
From a sketch by Dr Sequeira.

occurs sometimes under a valve-like fold on the left side, and in one instance there was such a cul-de-sac on each side, a centimetre long on the left and 6 millimetres long on the right.

The bottom of the cul-de-sac appeared in some instances to be closed by a kind of scar tissue, represented by puckered ridges of endocardium.

3. *The fossa ovalis and annulus* present many varieties. There was no trace of an annulus in eleven cases, and in a large proportion of cases it was ill-developed. In no case where the annulus was absent was there a patency.

The annulus was fenestrated in three cases. The floor of the fossa is often irregular, being crossed by thickened bands of endocardium, and puckered up like scar-tissue. This condition is always more marked on the right side. The appearance suggests the closure of the foramen by a process akin to inflammation.

The largest fossæ I have measured were 3·75 centimetres across (two cases), and the smallest (in a boy of 14) was 6 millimetres in diameter.

4. The *Eustachian valve* was definitely fenestrated in eleven cases, and was cribriform in one.

The orifice of the valve was crossed by endocardial, strap-like bands in five instances.

5. *Endocardial bands*, under which a probe could be passed, were present in the auricles in fifteen cases (including the five mentioned above). They are most commonly met with on the right side, crossing the orifices of two adjacent venæ Thebesii, and also occur attached to the edge of the annulus.

There were two long intra-ventricular bands, both occurring in the left ventricle, and attached just below the aortic valve. They resembled chordæ tendineæ. One was 4·2 centimetres long.

6. *Valves*.—In only one case, a male aged 25, were the valves abnormal. The anomaly was an aortic orifice, guarded by two semilunar valves only.

Other points noticed.—In three cases (infants) the ductus arteriosus was patent, viz., a female aged 2 days, a male aged 5 days, and

a female aged 12 days. In the last case the ductus was much contracted, but a fine probe passed along it.

In one case the left auricular appendix was subdivided by a septum into two unequal parts.

Including Dr Sequeira's cases, we have altogether records of 399 observations: of these 248 are on males and 151 on females.

Of the 399, there was an aperture of communication between the two auricles in 104 (26 per cent.).

In the 248 males there was a patency in 60 (24·2 per cent.), while in the 151 females it was present in 44 (29 per cent.).

TABLE I.—*Frequency of Patent Foramen Ovale.*

1. In all cases . . .	26	per cent.
2. In males . . .	24·2	„ „
3. In females . . .	29	„ „

It will thus be seen that the percentage is greater in females than in males.

The fact that the percentages of the total number of cases work out lower than those of Dr Sequeira is probably explained by the fact that he had the opportunity of examining the hearts of a comparatively larger number of children.

The effect which age has upon the patency of the foramen may be arrived at from the following table:—

TABLE II.—*Influence of Age on the Foramen Ovale.*

Age.	Male.			Female.		
	Cases.	Patent.	Percentage.	Cases.	Patent.	Percentage.
Under 1 year	3	3	100	7	6	88·8
Between 1 and 5	14	7	50	9	5	55·5
„ 5 „ 10	7	1	14·3	2	1	50
„ 10 „ 20	15	4	26·6	15	3	20
„ 20 „ 30	20	5	25	26	6	23
„ 30 „ 40	30	7	23·3	25	5	20
„ 40 „ 50	41	12	29·2	31	5	16·1
„ 50 „ 60	35	8	22·8	21	4	19
„ 60 „ 70	29	7	24	12	5	41·6
Over 70	12	3	25	4	2	50

The number of cases in which the age is recorded is, perhaps, too small for us to expect to get any very satisfactory percentages: if we add together the male and female cases, however, we shall get something more reliable.

TABLE III.—*Influence of Age on the Foramen Ovale in Males and Females combined.*

Age.		Percentage of Patent Foramina.				
Under	1 year	94·4
Between	1 and 5	52·75
"	5 " 10	32·15
"	10 " 20	23·3
"	20 " 30	24
"	30 " 40	21·65
"	40 " 50	22·65
"	50 " 60	20·9
"	60 " 70	32·8
Over	70 "	37·5

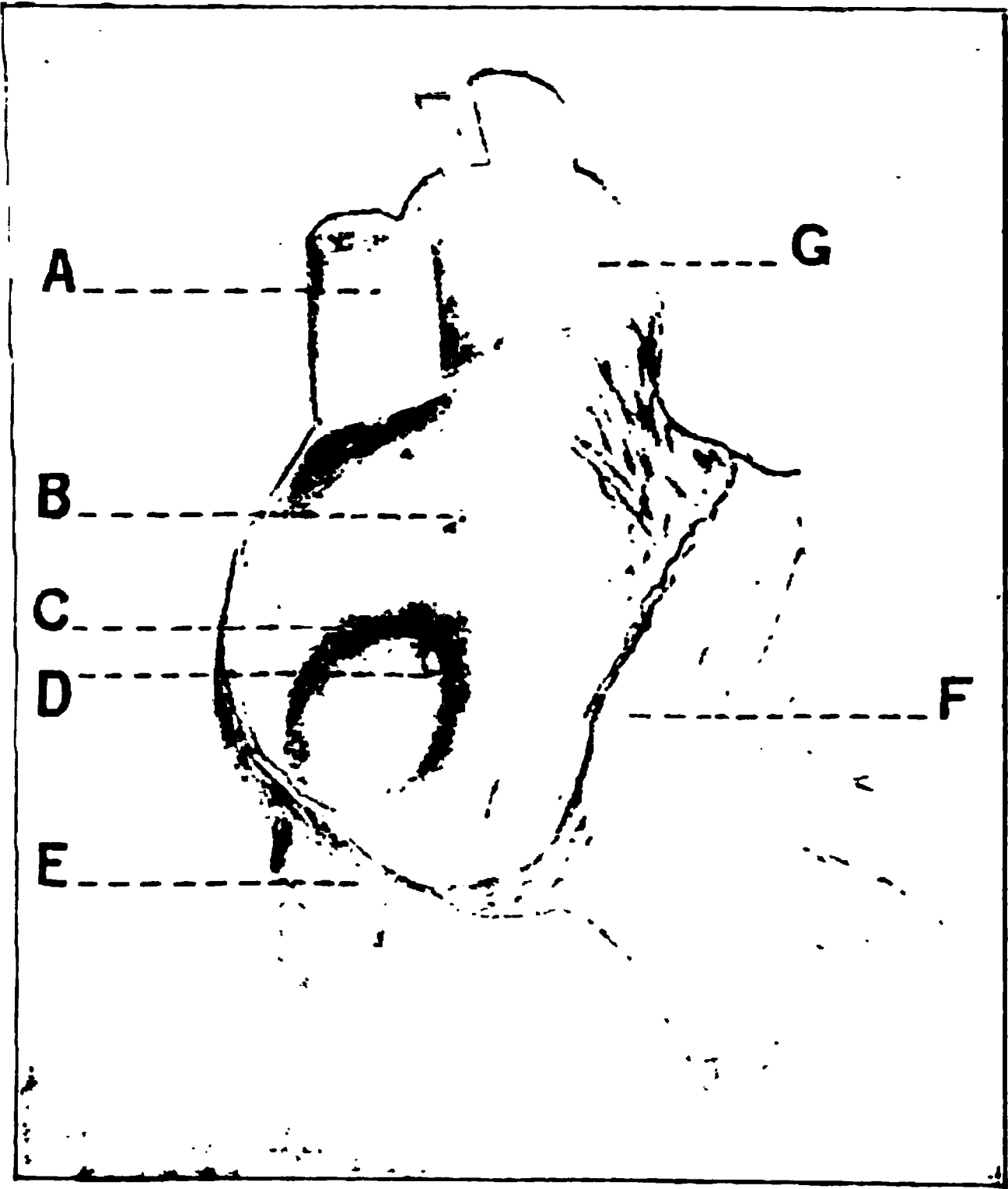


FIG. 2.—Position of the patency in the Fossa Ovalis. From a sketch by Mr Prentice, Liverpool.—A, superior vena cava ; B, foramina Thebesii ; C, annulus ovalis ; D, patency ; E, inferior vena cava ; F, auriculo-ventricular septum ; G, aorta.

From this it appears that the frequency of a persistent foramen is very great in children under 1 year, and that it steadily decreases until the age of 20 is reached, after which it persists in about 25 per cent. of all cases.

In 56 additional records the exact ages of the subjects are not mentioned, but it is stated that they are adult: if by this we may understand that over 20 is meant, we may use them for our inquiry.



FIG. 3.—Fenestrated Fossa Ovalis. From a sketch by Dr Smyth, of Queen's College, Belfast.

Of these 56 records, 7 (12·5 per cent.) have patent foramina. In Table III. the percentage of patencies in all the subjects over 20 comes to 26·6 per cent. The mean of these two observations gives us 19·5 per cent., or practically 20 per cent., as the number of times in which we may expect to find a patent foramen in an adult heart.

With regard to the nature of the patency, all our observations bear out the description already given by Dr Sequeira. Mr Prentice of

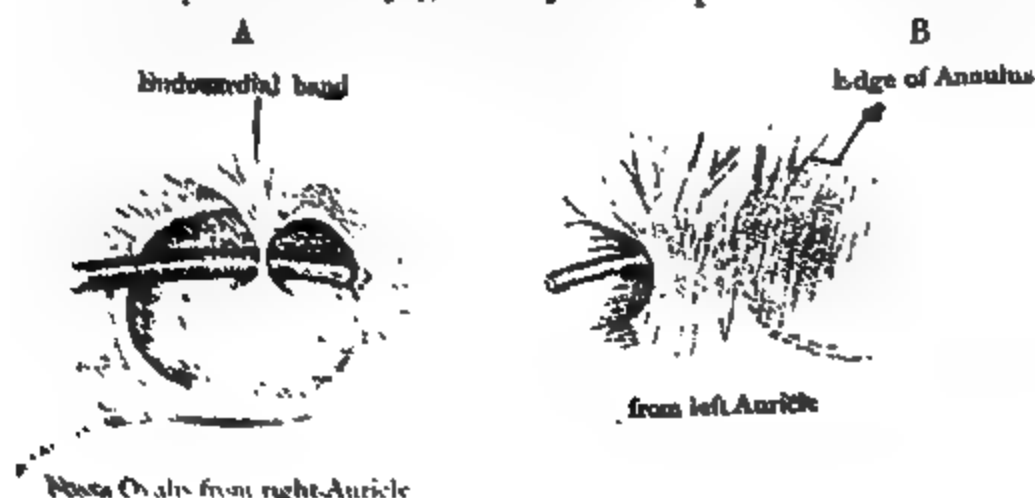


FIG. 4. Patent Fossa Ovalis, with endocardial band. From a sketch by Dr Madge Maclean, of Queen Margaret's College, Glasgow.

Liverpool points out that, when the heart is placed in its proper position, the opening is in the upper and left quadrant of the fossa ovalis—that is to say, under the point of greatest convexity of the annulus.

In a few cases a fenestrated floor was found in the fossa ovalis: in these, most of the openings seemed to be in the lower part of the septum atriorum.

Occasionally endocardial bands are found stretching from the floor of the fossa ovalis to the annulus, as in fig. 4.

Sometimes they stretch from one part of the annulus to another, as in fig 5.

With regard to the size of the opening, when it is present, we are

FIG. 5.—Endocardial band across the Fossa Ovalis. From a sketch by Dr Smyth, of Queen's College, Belfast.

only able to amplify Dr Sequeira's observations to a small extent, because many of our contributors have contented themselves with merely stating that the foramen was small or large, as the case might be. In 24 cases, however, the measurements are given, and in the following table we add these to Dr Sequeira's returns:—

TABLE IV.—*Size of the Opening between the Auricles.*

Measurement.	No. of Cases.	Percentage.
Under 2 mm.	11	13
Over 2 "	11	13
" 2.5 "	11	13
" 3 "	7	8.2
" 4 "	3	3.5
" 5 "	17	20
" 6 "	7	8.2
" 7 "	3	3.5
" 8 "	13	15.3
" 1 cm.	1	2.3

It will thus be seen that the opening may be of any size from a pin-hole to a centimetre.

SUMMARY OF QUESTION I.

1. An opening between the two auricles occurs in about a quarter of all cases, though probably, owing to its valvular nature, no blood passes through it.

2. It is somewhat more frequent in females than in males.

3. It is very frequent indeed in children under one year: after this its frequency decreases until the age of 20 is reached.

4. In adults over 20 the opening occurs about once in five cases.
5. The opening is situated in the upper and left quadrant of the fossa ovalis.
6. Its size varies from 1 to 10 mm.

QUESTION II.

The arrangement and number of the lymphatic glands accompanying the common external and internal iliac arteries.

Observations were received from :—

Dr Johnstone, Queen's College, Belfast; Mr H. P. Packenridge, Middlesex Hospital; Mr C. Hadley, Mason College, Birmingham; Mr A. Keith, London Hospital.

The difficulty of making a complete examination of the arrangement of the lymphatic glands along the iliac vessels, without disturbing the normal course of dissection, accounts, in a great measure, for the small number of returns on this question. The material¹ examined may be stated in tabular form thus :—

	Right Side.	Left Side.
Males . . .	52	29
Females . . .	25	17

Counting right and left sides separately, 123 observations were made: both sides were examined in 29 males and 17 females, 23 males and 9 females having been examined on the right side only. So far as this limited number of observations goes, it shows that—

- (1) The arrangement of glands on the right and left side of the same pelvis is not, as a rule, symmetrical: they are rather more numerous on the right side.
- (2) There is a considerable difference between the arrangement in one body and another, both as to the number and position of the glands.
- (3) The arrangement in male and female bodies shows no material difference in the position of the glands, but they are perhaps more numerous in the male than in the female.
- (4) The glands in children at birth, as in many of the lower primates throughout life, form an almost continuous chain; they are frequently of small size and very few in number in old people.
- (5) The glands are not usually so abundant as represented by Mascagni, from whose works most modern accounts are taken.
- (6) Our statistics give us no data for drawing conclusions as to the influence of disease.

Owing to the absence of a nomenclature, which would be of inestimable convenience if each gland were designated according to the

¹ In order to assure ourselves that the grouping of glands here employed was a natural one, the arrangement in an orang, three macaques, and three ceropithecques was examined.

organ or region it receives lymph from, we have been obliged to use the accompanying diagram to indicate the glands more frequently

FIG. 6.—Diagram of the Iliac Glands.

A. Femoral collecting.	F. Mesial external iliac.	L. Pudo-eratic.
B. Deep epigastric.	G. Inter iliac.	M. Gluteal.
C. Supracrural.	H. Obturator.	N. Mesial common iliac.
D. Lateral external iliac.	K. Hypogastric.	P. Subaortic.
E. Lateral common iliac.		

present. The glands on the right side are marked by capitals, those on the left by italics. It will be seen that we tentatively propose a nomenclature.

Gland 'A' (femoral collecting gland):—

	Right Side.		Left Side.	
	Present.	Absent.	Present.	Absent.
Males	47	5	23	4
Females	18	7	9	8

It is present very generally in the primates: it was observed in an orang, in three macaques, and two out of three cercopithecques. A leash of vessels can be seen coming to it from the superficial inguinal glands. In three males, on the right side, it was represented by two glands.

Gland 'B' (deep epigastric gland):—

	Right Side.		Left Side.	
	Present.	Absent.	Present.	Absent.
Males	16	36	15	12
Females	8	17	7	10

This gland was not found in any of the primates examined. It appears to receive the lymphatics accompanying the deep epigastric vessels. It is more frequently absent in man than present, and is of small size.

Gland 'C' (supracrural gland):—

	Right Side.		Left Side.	
	Present.	Absent.	Present.	Absent.
Males	34	18	19	8
Females	11	14	8	9

This gland is usually of large size, and receives the deep femoral lymphatics through the crural canal. The lower end of this gland occasionally projects into that canal, and evidently represents the gland which is usually described as being situated within it. This gland may lie close to the external iliac vein, but frequently it is depressed within the pelvis, almost in contact with the obturator nerve. The vessels leaving it go mostly to the gland lying in the angle between the external and internal iliac arteries, marked 'G' in the diagram (interiliac gland). These two glands, 'C' and 'G,' are occasionally continuous. This gland was observed in all the primates examined (1 orang, 3 macaques, and 3 cercopithecques). In two male bodies, one on the right side, the other on the left, there were two glands in this situation.

Glands 'D' (lateral external iliac glands):—

	Right Side.		Left Side.	
	Present.	Absent.	Present.	Absent.
Males	39	13	17	10
Females	12	13	7	10

The glands lying along the outer side of the external iliac artery, or in front of that artery, as they are occasionally, are commonly two in number, but not infrequently there is only one; or there may be, as is frequently the case in very young children and lower primates generally, a chain of glands.

Glands 'E' (lateral common iliac glands):—

	Right Side.		Left Side.	
	Present.	Absent.	Present.	Absent.
Males	47	5	26	1
Females	24	1	14	3

This is the most constant group of glands about the pelvis, although it is subject to much variation as to the number and position of its constituent glands. The lowest gland of the group commonly lies with its lower end between the common iliac artery, at its point of bifurcation, and the brim of the pelvis, being occasionally almost continuous with gland 'G,' from which it receives vessels, both over and beneath the common iliac vessels. The highest gland of the group lies in front of the inferior vena cava. The vessels from the glands 'E' pass to the glands by the side of the vena cava 'Q' (caval glands), and pre-aortic 'R,' while the vessels from 'E' (on the left) pass to the glands 'S' (lateral aortic glands) by the side of the aorta. This group of glands lies more posteriorly to the common

iliac artery on the left than on the right. They number equally frequently two or three, but in women and young children are often more numerous, at times forming a chain.

Gland 'F' (mesial external iliac gland):—

	Right Side.		Left Side.	
	Present.	Absent.	Present.	Absent.
Males	21	31	14	13
Females	8	17	7	10

The gland lies sometimes on the external iliac vein, as represented in the diagram, but quite as frequently it is seated more deeply in the pelvis, some way below the vein. Sometimes there are two glands in this position: they receive the vessels from the gland 'C.' It is more frequently absent than present.

Glands 'G' (interiliac glands):—

	Right Side.		Left Side.	
	Present.	Absent.	Present.	Absent.
Males	40	12	19	8
Females	19	6	13	4

This is undoubtedly the most important group of pelvic glands: it receives lymph from the lower parts of the genito-urinary track, besides the lymph from gland 'C.' The position of the group is fairly constant in the angle between the external and internal iliac arteries. From these glands the lymphatic vessels pass to group 'E.' There is commonly only one gland, a large one, but not infrequently there are two, three, four, or a group of numerous small glands.

Gland 'H' (obturator gland):—

	Right Side.		Left Side.	
	Present.	Absent.	Present.	Absent.
Males	3	49	2	25
Females	2	23	—	17

This gland, the obturator, is rarely present. It is a very small one, and lies above and outside the obturator nerve and vessels, where they make their exit from the pelvis. It was present in both right and left sides of the orang, but not in any of the other primates examined.

Gland 'K' (hypogastric gland):—

	Right Side.		Left Side.	
	Present.	Absent.	Present.	Absent.
Males	9	43	5	22
Females	2	23	5	12

This gland lies on or near the anterior division of the internal iliac artery, near the point of origin of the superior vesical artery. It is

much more frequently absent than present. There is commonly only one gland, but on four occasions this was represented by two, and on two occasions by three glands. The number of glands appears to have no reference to the sex of the individual. This group was found in all the primates examined.

Gland 'L' (pudo-sciatic gland):—

	Right Side.		Left Side.	
	Present.	Absent.	Present.	Absent.
Males	7	45	4	23
Females	2	23	3	14

Only in one case were there two glands, in all the others only one. It lies behind the anterior division of the internal iliac artery, near the origin of the sciatic artery, probably deriving its lymph from the areas supplied by the pudic and sciatic arteries. It is much more frequently absent than present, but may easily escape notice unless specially sought for. It was found in the primates examined.

Gland 'M' (gluteal gland):—

	Right Side.		Left Side.	
	Present.	Absent.	Present.	Absent.
Males	15	37	7	20
Females	8	17	4	13

This gland (in only two cases were there two) lies behind the internal iliac artery, above and somewhat external to the point of origin of the gluteal artery. It receives lymph probably from the area supplied by that artery. It is rather more frequently absent than present; it was found in most of the primates examined.

Gland 'N' (mesial common iliac glands):—

	Right Side.		Left Side.	
	Present.	Absent.	Present.	Absent.
Males	16	36	10	17
Females	11	14	6	11

This group is variable, both in number and position, but the more common number is two, and the more usual position is on the common iliac vein, close by the side of the common iliac artery. There is frequently only one, and rarely three or more. Sometimes the gland lies between the vessels and the brim of the pelvis, and is then hard to differentiate from the group 'E,' along the outer side of the common iliac artery. The glands 'N' receive vessels from the glands 'L' and 'M.' This group is generally represented in primates.

Glands 'P' (sub-aortic glands):—

	Right Side.		Left Side.	
	Present.	Absent.	Present.	Absent.
Males	12	40	5	22
Females	6	19	4	13

There may be, with almost equal frequency, one, two, or three glands in this group. It is situated in the fork between the common iliac arteries, and on the left common iliac vein. It receives some of the vessels from the glands 'N,' and its vessels pass mostly to the pre-aortic glands.

Sacral glands are rarely present, at any rate of a size that can be easily seen by the naked eye: they were not observed once in thirty bodies from which the rectum had been removed. There are many glands in the meso-rectum, and on the sacral surface of the second part of the rectum, but these are hæmorrhoidal, and not sacral glands.

QUESTION III.

The position of the spinal accessory nerve. Whether it passes outward between the jugular vein and internal carotid artery, or between the jugular vein and the atlas? Whether it perforates the sterno-mastoid or not: if so, does the whole nerve perforate, or only a part? Which division of the sterno-mastoid does it perforate?

Replies have been received from the following:—

Dr Low, Aberdeen University; Mr H. Pringle, Dublin University; Dr Haygarth, Edinburgh University; Dr Johnstone, Queen's College, Belfast; Dr Madge Maclean, Queen Margaret College, Glasgow; Mr Prentice, University College, Liverpool; Mr H. Brawn, Mason College, Birmingham; Dr Hamilton, Guy's Hospital; Mr Keith, London Hospital; Mr Furnivall, St Bartholomew's Hospital; Mr H. Clarke, St Thomas's Hospital; Dr Tims and Mr Dawson, Westminster Hospital.

In the first place, we propose to consider the relation of the nerve to the jugular vein: to do this we have 223 records of observations on the right, and 209 on the left side. In 42 other observations the side is not stated. These figures added together give a total of 474 observations on the right and left sides. Of these, the nerve passed in front of the vein, i.e. between the vein and the internal carotid artery (prejugular), in 332 cases (70 per cent.). In 127 cases (26·8 per cent.) it passed behind the vein, i.e. between the vein and the atlas (postjugular), while in 5 cases (3·2 per cent.) the nerve pierced the internal jugular vein¹ (intrajugular).

TABLE I.—*Frequency of the Pre-, Post-, and Intra-jugular Courses of the Eleventh Nerve in all cases (both sides).*

Prejugular	70	per cent.
Postjugular	26·8	„ „
Intrajugular	3·2	„ „

¹ In those cases in which the nerve appears to pierce the vein it does not really do so: what happens is, that the formative tributaries of the internal jugular, the lateral and inferior petrosal sinuses, have not yet united, but are bound together by fibrous tissue; through this tissue the spinal accessory passes.

With regard to the influence which the side of the body exerts on the relative frequency of these relations, we have, as above stated, 223 observations on the right side and 209 on the left.

Of the 223 on the right, we find that 155 (60·5 per cent.) were prejugular, 66 (29·6 per cent.) postjugular, and 2 (·9 per cent.) intrajugular.

Of the 209 observations on the left, 142 (67·9 per cent.) were prejugular, 65 (31·1) postjugular, and 2 (1 per cent.) intrajugular.

TABLE II.—*Relation of the Eleventh Nerve to the Vein on the two sides.*

	Right.	Left.
Prejugular	69·5 per cent.	67·9 per cent.
Postjugular	29·6 „ „	31·1 „ „
Intrajugular	·9 „ „	1·0 „ „

This table shows that the side has practically no influence on the relation of the nerve to the vein.

Our statistics show that the relation of the nerve to the vein is not always, nor even frequently, alike on the two sides of the same body. The intrajugular course was never seen on both sides of the same body.

With regard to the influence of sex, there are 107 observations on the right side in males, and 73 in females. Of the 107 in males, 77 (71·9 per cent.) are prejugular, 29 (27·1 per cent.) postjugular, and 1 (1 per cent.) intrajugular.

Of the 73 females, 46 (63 per cent.) have the nerve taking a prejugular course, 26 (35·6 per cent.) a postjugular, and 1 (1·4 per cent.) an intrajugular.

On the left side, there are observations of 106 males and 68 females. Of the 106 males, 75 (70·8 per cent.) are prejugular, 31 (29·2 per cent.) postjugular, and none intrajugular.

Of the 68 females, 47 (69·1 per cent.) are prejugular, 21 (30·9 per cent.) postjugular, and none intrajugular.

TABLE III.—*Influence of Sex on the relation of the Nerve to the Vein on the right side.*

	Male.	Female.
Prejugular	71·9 per cent.	63 per cent.
Postjugular	27·1 „ „	35·6 „ „
Intrajugular	1 „ „	1·4 „ „

TABLE IV.—*Influence of Sex on the relation of the Nerve to the Vein on the left side.*

	Male.	Female.
Prejugular	70·8 per cent.	69·1 per cent.
Postjugular	29·2 „ „	30·9 „ „
Intrajugular	—	—

From these tables it would appear that the postjugular course of the nerve is somewhat more common in females than in males.

The next point to be considered is the relation of the spinal accessory nerve to the sterno-mastoid muscle. Under this heading we shall first find out how often the nerve pierces the muscle. The total number of observations, on both sides, in male and female subjects, as well as those in which the side and sex are not stated, is 415. In 341 of these (82·2 per cent.) the whole or part of the nerve pierces the muscle, in 72 (17·3 per cent.) the nerve passes deep to the muscle, and in 2 cases (·5 per cent.) (opposite sides of the same body) it ends in the sterno-mastoid.

TABLE V.—*Frequency with which the Eleventh Nerve pierces the Sterno-mastoid Muscle in all cases (both sides).*

Perforates	82·2 per cent.
Passes deep	17·3 „ „
Ends in muscle	·5 „ „

With regard to the influence of side, there are 193 observations on the right and 178 on the left.¹

Of the 193 on the right, 161 (83·5 per cent.) pierce the muscle, and 32 (16·5 per cent.) pass deep to it. Of the 178 observations on the left side, 150 (84·3 per cent.) pierce the muscle, and 28 (15·7 per cent.) pass deep.

TABLE VI.—*Frequency with which the Spinal Accessory pierces the Sterno-mastoid on the two sides.*

	Right.	Left.
Perforates	83·5 per cent.	84·3 per cent.
Passes deep	16·5 „ „	15·7 „ „

This table shows that the side has no appreciable influence on the course of the nerve.

In order to test whether sex affects the relation of the nerve to the muscle, there are records of 192 observations in males on both sides, and 129 of females.

Of the 192 males the nerve pierced the muscle in 154 (80·2 per cent.), while in the 129 females the muscle was pierced 116 times (89·9 per cent.).

TABLE VII.—*Influence of Sex on the relation of the Spinal Accessory to the Sterno-mastoid (both sides taken together).*

	Male.	Female.
Perforates	80·2 per cent.	89·9 per cent.
Passes deep	19·8 „ „	10·1 „ „

¹ Neglecting the one case in which the nerve ended in the muscle.

This difference of nearly 10 per cent. between the two sexes is certainly noteworthy, especially as the averages are taken from a fair number of observations.

The next point to determine is how often the whole nerve pierces the sterno-mastoid, and how often only a part of it does so. We have already stated that the nerve pierced the muscle 161 times out of 193 observations on the right side, and 150 times out of 178 observations on the left.

Of the 161 cases in which the nerve pierced the sterno-mastoid on the right side, the whole nerve pierced in 160, while in 1 case part of the nerve pierced the muscle and the rest passed deep to it.

Of the 150 cases on the left side, the whole nerve pierced the muscle 147 times, while in 3 instances only part pierced it. It will thus be seen that in somewhere about 1 per cent. of the cases in which the nerve pierces the muscle, it is not the whole nerve which does so.

As it has occurred to us that the nerves which have a postjugular course would, by reason of their greater depth, be more likely to pass deep to the sterno-mastoid instead of piercing it, we have picked out all the nerves passing deep to the muscle which have also their relation to the vein recorded. Out of 72 of these, 41 (57 per cent.) are prejugular and 31 (43 per cent.) postjugular. In the same way, out of 341 nerves piercing the sterno-mastoid, 255 (74·8 per cent.) are prejugular and 86 (25·2 per cent.) postjugular.

TABLE VIII.—*Frequency with which Non-perforating Nerves are also Postjugular.*

	Prejugular.	Postjugular.
Perforating	74·8 per cent.	25·2 per cent.
Non-perforating	57 „ „	43 „ „

It will thus be seen that nerves which pass deep to the sterno-mastoid are more likely to be postjugular than those which pierce the muscle.

It has already been stated that in 341 cases out of 415 the spinal accessory pierced the sterno-mastoid: in 271 of these the part of the muscle pierced is recorded, and we find that in 258 (95·2 per cent.) the nerve pierced the clavicular head. In 8 cases (3 per cent.) the sternal head was the part pierced, in 1 case both the sternal and clavicular parts of the muscle were pierced, while on 4 occasions (1·5 per cent.) the nerve passed between the sternal and clavicular heads.

TABLE IX.—*Frequency with which the different parts of the Sterno-mastoid are pierced.*

Clavicular head	95·2 per cent.
Sternal head	3 „ „
Both heads	1 case
Passes between the two	1·5 per cent.

The one case in which the nerve pierced both heads was described by Mr Prentice of Liverpool, whose sketch we reproduce: it will be seen that the nerve passed deep to the sterno-mastoid proper, and superficial to the sterno-occipital, *i.e.* it pierced the sternal head of

FIG. 7.—Spinal Accessory Nerve piercing both heads of the sterno-mastoid.
From a sketch by Mr Prentice, Liverpool.

the sterno-cleido-mastoid. It then passed deep to the cleido-occipital and superficial to the cleido-mastoid, thus piercing the clavicular head also.

SUMMARY OF QUESTION III.

1. The spinal accessory nerve passes most frequently in front of the internal jugular vein, less frequently behind, and very occasionally through it.
2. The side of the body makes no difference to these relations.
3. The postjugular course of the nerve is somewhat more common in females than in males.
4. In 82 per cent. of all cases the nerve pierces the sterno-mastoid muscle.
5. The side of the body makes no difference to this percentage.
6. In females the nerve pierces the muscle more frequently than in males.
7. Very occasionally (about 1 per cent.) the nerve divides, and only its superficial part pierces the muscle.
8. When the nerve passes deep to the sterno-mastoid, it is more likely to have a postjugular course than if it pierced the muscle.
9. In almost every case it is the clavicular head of the muscle which is pierced by the nerve.

QUESTION IV.

The presence of sesamoid bodies in either head of the gastrocnemius, and in the tendon of the peroneus longus. If possible, the nature of these bodies (fibrous, fibro-cartilaginous, cartilaginous, or osseous) should be stated.

Returns have been received from the following :—

Dr A. Low, Aberdeen University; Mr E. F. Stapleton, Dublin University; Dr R. Haygarth, Edinburgh University; Dr R. J. Johnstone, Queen's College, Belfast; Dr Madge Maclean, Queen Margaret's College, Glasgow; Mr W. Billington, Mason College, Birmingham; Mr Prentice, University College, Liverpool; Dr F. J. Steward, Guy's Hospital; Mr H. E. Ridewood, London Hospital; Mr H. P. Pankridge, Middlesex Hospital; Dr Tims and Mr Dawson, Westminster Hospital.

The evidence on this question may be divided into two parts: firstly, that of the gastrocnemius; and secondly, that of the peroneus longus.

In the case of the gastrocnemius there is a total of 195 observations. In 161 the side and sex are stated, in 27 the sex is not recorded, while in 7 no mention is made of the side.

Taking the side into consideration in the first place, we find that there is a total of 146 complete observations of male and female subjects on the right, and of 141 on the left.

Of the 146 observations on the right side, 6 (4·1 per cent.) show the presence of sesamoid bodies in both heads of the gastrocnemius, 37 (25·3 per cent.) in the outer head only, and 12 (8·2 per cent.) in the inner head only.

Of the 141 observations on the left side, 10 (7 per cent.) show sesamoid bodies in both heads, 28 (19·8 per cent.) in the outer head only, and 11 (7·8 per cent.) in the inner head only.

With regard to the influence of sex, there are 80 observations of males on the right side and 77 on the left.

On the right side in the males a sesamoid body was present in both heads of the gastrocnemius in 5 cases out of the 80 (6·3 per cent.).

It was present in the outer head only in 22 (27·5 per cent.), while in the inner head only it was present in 8 cases, or 10 per cent.

On the left side in the males a sesamoid body was present in both heads in 6 cases out of the 77 (7·8 per cent.). It was present in the outer head only in 16 (20·8 per cent.), while in the inner head only it was present in 8 cases, or 10·4 per cent.

There are 44 observations of females on the right side, and 40 on the left.

Of the 44 on the right, a sesamoid body was not found in both heads in any case. It was present in the outer head alone in 11 cases (25 per cent.), and in the inner head alone in 2 cases (4·5 per cent.).

Of the 40 observations on the left side a sesamoid body was present in each head in 2 cases (5 per cent.), in the outer head alone in 8 (20 per cent.), and in the inner head alone in 2 (5 per cent.).

These figures will perhaps convey more if they are arranged in a tabular form.

TABLE I.—*Frequency of Sesamoids in the Gastrocnemius, total observations (♂ and ♀).*

	Right.	Left.
Both heads	4·1 per cent.	7 per cent.
Outer head only	25·3 „ „	19·8 „ „
Inner head only	8·2 „ „	7·8 „ „

By adding the percentage of both heads to that of the outer or inner head only the total percentage for either head may be found.

TABLE II.—*Total frequency of Sesamoids in the two heads of the Gastrocnemius.*

	Right.	Left.
Outer head	29·4 per cent.	26·8 per cent.
Inner head	12·3 „ „	14·8 „ „

These tables point to the fact that sesamoid bodies are most common in the outer head only, then in the inner head only, and least common in both heads.

TABLE III.—*Frequency of Sesamoids in the Gastrocnemius of Males.*

	Right.	Left.
Both heads	6·3 per cent.	7·8 per cent.
Outer head only	27·5 „ „	20·8 „ „
Inner head only	10 „ „	10·4 „ „

TABLE IV.—*Frequency of Sesamoids in the Gastrocnemius of Females.*

	Right.	Left.
Both heads	—	5 per cent.
Outer head only	25 per cent.	20 „ „
Inner head only	4·5 „ „	5 „ „

These tables, to our minds, show that sex has little influence on the frequency of sesamoid bodies, though they may possibly be less frequent in the inner head and in both heads together in females than in males, and thus may be said to be less frequent altogether in females than in males.

With regard to the constitution of the bodies, we have evidence that in many of the investigations no microscopical examination was made : we shall therefore content ourselves with dividing the cases in which sesamoid bodies occur into two classes,—firstly, those in which the bodies were osseous ; secondly, those in which they were of some other material (fibrous, fibro-cartilaginous, or cartilaginous).

Taking males and females together, sesamoids were found, on the right side, 43 times in 146 observations of the outer head, and 18 times in the inner head. On the left side, out of 141 observations, they were found 38 times in the outer and 21 times in the inner head.

Of the 43 sesamoid bodies in the outer head of the right gastrocnemius, 16 (37·2 per cent.) were osseous and 27 (62·8 per cent.) non-osseous.

Of the 18 sesamoids in the inner head of the right gastrocnemius, 1 (5·5 per cent.) was osseous and 17 (94·5 per cent.) non-osseous.

Of the 38 sesamoids in the outer head of the left gastrocnemius, 12 (31·5 per cent.) were osseous, and 26 (68·5 per cent.) non-osseous.

Of the 21 sesamoids in the inner head of the left gastrocnemius, 2 (9·5 per cent.) were osseous and 19 (90·5 per cent.) non-osseous.

TABLE V.—*Structure of the Sesamoid bodies in the right Gastrocnemius.*

	Outer Head.	Inner Head.
Osseous	37·2 per cent.	5·5 per cent.
Non-osseous	62·8 „ „	94·5 „ „

TABLE VI.—*Structure of the Sesamoid Bodies in the left Gastrocnemius.*

	Outer head.	Inner head.
Osseous	31·5 per cent.	9·5 per cent.
Non-osseous	68·5 „ „	90·5 „ „

These tables show that sesamoids in the gastrocnemius are more often fibrous than osseous, that they are more often ossified in the outer head than in the inner, and that the side has little, if any, influence on their structure.

To ascertain whether sex has any influence on the ossification of these bodies, we have taken the total number in both heads and on both sides. This gives us 79 bodies in male subjects and 28 in female.

Of the 79 sesamoids found in male bodies, 22 (28·1 per cent.) were osseous and 57 (71·9 per cent.) non-osseous.

Of the 28 sesamoids found in female bodies, 10 (35·7 per cent.) were osseous and 18 (64·3 per cent.) non-osseous.

TABLE VII.—*Structure of Sesamoids in the two Sexes.*

	Male.	Female.
Osseous	28·1 per cent.	35·7 per cent.
Non-osseous	71·9 „ „	64·3 „ „

As far, therefore, as our small number of observations goes, it would appear that sesamoid bodies in the gastrocnemius are more frequently ossified in women than in men. Upon the influence of age we have no statistics, though this perhaps is the less to be regretted, since most of the bodies were probably those of old people.

COMPARATIVE ANATOMY NOTE.

The sesamoid bodies in the heads of the gastrocnemius are of course homologous with the fabellæ of the lower mammals: these bones articulate with the upper and back part of the condyles of the femur, and are developed in the posterior part of the capsule of the knee-joint. Throughout the mammalian series the external fabella is usually the better developed, and often it is the only one present: in some kangaroos it is so large that it articulates with the fibula during flexion of the knee.

Among the primates, fabellæ are found in both heads of the gastrocnemius in lemurs and cynomorphous monkeys. In the chimpanzee a cartilaginous fabella occurs in the inner head only. In the gibbon it may be present or absent, in either or both heads, as in man. In the orang and the gorilla no sesamoids have been observed.

PERONEUS LONGUS.

The second part of the question deals with the sesamoid body in the tendon of the peroneus longus, where it turns round the lower and outer edge of the cuboid.

Altogether we have 124 observations on the right side and 121 on the left.

Of the 124 tendons on the right, 92 (74·2 per cent.) contained a sesamoid; and of the 121 on the left, sesamoid bodies were found in 91 (75·2 per cent.).

We are of opinion that too much reliance should not be placed on these figures, since the presence or absence of a fibrous sesamoid in a fibrous tendon is often a question of individual opinion. Some observers have sent us returns with long sequences of cases in which no sesamoid was noticed, while others have found a sesamoid of some kind in every case examined. Although the recognition of the presence or absence of a sesamoid may be, and probably is, a question of individual taste, there can be no room for doubt as to the number of cases in which a bony deposit was found in the tendon; and we find that, out of the 124 tendons on the right side, the sesamoid was ossified in 25 (20·2 per cent.), while of the 121 on the left there was a bony deposit in 24 (19·8 per cent.).

TABLE VIII.—*Frequency of Sesamoids in the Tendon of the Peroneus Longus.*

	Right.	Left.
Sesamoids of any kind	74·2 per cent.	75·2 per cent.
Osseous	20·2 " "	19·8 " "
Non-osseous	54 " "	55·4 " "

This table shows that, in the bodies examined, bony sesamoids were practically as common on the left as on the right.

It must be borne in mind, in reading these returns, that the greater number of subjects examined were advanced in years.

Our statistics show that the sesamoids are not always, nor even frequently, of the same structure on the two sides of the same body. With regard to the influence of sex on the structure of the sesamoid bodies, we have records of 77 observations on the right side in male subjects and of 76 on the left.

Of the 77 tendons on the right, 18 (23·3 per cent.) contained bony sesamoids, while of the 76 on the left, 17 (22·3 per cent.) contained them.

In female subjects we have 47 observations on the right side and 44 on the left.

Of the 47 on the right, a bony sesamoid was present in 8 (17 per cent.), while among the 44 on the left it was found in 7 (16 per cent.).

TABLE IX.—*Frequency of bony Sesamoids in the Peroneus Longus of the two Sexes.*

	Right.	Left.
Male	23·3 per cent.	22·3 per cent.
Female	17 „ „	16 „ „

From this it seems that in males ossification is more frequent than in females.

SUMMARY OF QUESTION IV.

A. 1. Sesamoid bodies are most frequently met with in the outer head of the gastrocnemius, then in the inner head, and least frequently in both heads.

2. They are rather more common on the right side than on the left.

3. Sex has little influence on their frequency.

4. The structure of these bodies is more often non-osseous than osseous; they are more likely to be ossified in the outer head than in the inner, but the side of the body has little influence on their structure.

5. The bodies are possibly more frequently ossified in women than in men.

B. 1. It is difficult in all cases to judge satisfactorily whether a fibrous sesamoid is or is not present in the tendon of the peroneus longus.

2. Bony sesamoids occur in some 20 per cent. of all cases, and they are as common on the left side as on the right.

3. They are rather more common in males than in females.

Journal of Anatomy and Physiology.

A THEORY OF MUSCULAR CONTRACTION.

By W. M'DOUGALL, M.A., M.B., B.Sc., *Fellow of St John's College, Cambridge.*

IN an article dealing with the structure of cross-striated muscle published in the April and July numbers of this *Journal*, I have briefly formulated a hypothesis as to the nature of the processes that immediately determine muscular contraction, and have stated that it is easy to offer plausible explanations, in terms of the hypothesis, of many of the properties and phenomena exhibited by cross-striated muscle. I wish to describe in this article certain observations that seem to give support to this hypothesis, and to show briefly how the hypothesis lends itself to these explanations.

I will first make some critical remarks on two hypotheses that claim to afford physical explanations of the process of muscular contraction; for these two hypotheses, suggested by Engelmann and Verworn respectively, are the most prominent of the many that are current at the present time.

Engelmann's Hypothesis.

Engelmann has recently made a suggestion as to the nature of muscular contraction,¹ and has offered to the Royal Society, in the Croonian Lecture of the year 1895, a 'proof' of the truth of the hypothesis (see *Nature*, 28th March 1895). The essence of the suggestion is, that contraction is caused by a heating of some small part of the fibrils of which he supposes the contractile substance of muscle to be made up. The 'proof' consists

¹ Ueber den Ursprung der Muskelkraft, 1893.

in the pointing out of certain striking resemblances between the properties of muscle and those of stretched violin-strings and other lifeless bodies of a similar nature.

Fick¹ has criticised the hypothesis, pointing out that the absolute force of the muscle is so much greater than that of any such system as Engelmann's muscle model, that the bounds of legitimate analogy are overstepped. Engelmann professes to have refuted this objection by pointing out the following facts, and making certain deductions from them: (a) that a violin-string .7 mm. in diameter will *perceptibly* raise a load of 1 kilo, when its temperature is rapidly raised to 130° C.; (b) that the maximum load that a tetanised strip of human muscle 1 sq. cm. in transverse section can raise is 10 kilo; (c) that in tetanus a muscle may rise 1° in temperature. From these figures he concludes that the string exerts twenty times as much force as the muscle of the same cross-section. But this conclusion cannot fairly be drawn from the figures. For let us assume that the string was raised only 100° C. in temperature. The area of its cross-section is nearly .5 sq. mm. Then the string .5 sq. mm. in cross-section raised 100° C. in temperature lifts 1 kilo. Engelmann supposes that parts of the muscle are directly heated while others are not, and the rise of the temperature which would give an efficiency of 30 per cent. (which is that of muscle)² is 100° C. Then let us suppose the temperature distributed in this most favourable manner, and we have for the muscle the figures 1.06 sq. cm. raised 100° C. in temperature lifts 10 kilos, i.e., the muscle exerts five times as much force as the string for equal cross-sections. There are two considerations which show that the data of this calculation, as given by Engelmann, are far too favourable for the string. In the first place, he has neglected the question of absolute force; and probably the muscle raises the weight to a height which is a much greater proportion of its own length than does the string. Secondly, the tetanus during which a muscle rises 1° C. in temperature is one continued for some minutes (*cf.* I., s. 158). Becquerel observed a rise of temperature of 1° C. after five minutes' tetanisation, and (s. 159) Helmholtz observed a rise of temperature of .18° C. on tetanis-

¹ Pflüger, *Arch.*, Bd. liii.

² I., s. 166. [I. refers here and hereafter to Hermann's *Handbuch d. Phys.*, ed. 1. II. refers to Biedermann's *Electro-Physiologie*, Eng. trans.]

ing frog's muscle for two or three minutes. The rise in temperature of the muscle during the actual raising of the weight is, therefore, certainly much less than 1° C., probably only a very small fraction of a degree. Allowing, then, for these considerations of the forces exerted by equal masses of equal cross-section of muscle and violin-string, raised equally in temperature, that of muscle must be at least 100 times greater than that of the string.

A similar conclusion may be more legitimately reached in this way: 1 sq. cm. of frog's muscle can raise in a simple contraction 400 grs. (I., s. 64), and the maximum rise of temperature for a simple contraction is $\cdot 001^{\circ}$ C.— $\cdot 005^{\circ}$ C. (I., s. 159); then taking the lower estimate, 1 sq. cm. of the muscle with rise of temperature $\cdot 001^{\circ}$ C. lifts 400 grs., *i.e.*, $\frac{1}{1000}$ sq. mm. rising 100° C. in temperature lifts 400 grs., and in the case of the string $\frac{1}{2}$ sq. mm. rising 100° C. in temperature lifts 1 kilo, *i.e.*, the muscle exerts the same pull with a cross-section about $\frac{1}{200}$ of that of the string, or, taking the higher estimate of the rise of temperature, about $\frac{1}{40}$ of that of the string. Here, again, the height to which the weight is lifted has been neglected; and if it were taken into account, the absolute force of the muscle would probably be found to be very much greater still in proportion to that of the string.

One of the most striking resemblances between living contractile structures and the lifeless substances with which the comparison is made, is the possession of doubly refracting parts by both classes; and Engelmann insists that one of the optic axes is always parallel to the direction of contraction. But he has pointed out, as particularly significant, the fact that in certain muscle fibres the contractile fibrils run in steep spirals round the fibres, their obliquity to the axis of the fibre increasing during contraction, while the optic axes of the fibrils remain parallel to the axis of the fibre in all degrees of contraction. He adds, "hence it is not the morphological axis of the fibrils, but the optical axis of their doubly refractive constituents which coincide with the direction of the contracting force." But the direction of the contracting force with which the optical axis of the fibrils coincides, is the resultant of the forces acting along the morphological axis of all the fibrils; for it cannot be contended

that the fibrils exert their pull in any other direction than along their morphological axes. These fibrils, then, form a notable exception to the law which Engelmann is attempting to establish, and prove that this point of resemblance between the two classes of objects is merely a coincidence. In just the same way all the other points of resemblance remain merely striking coincidences, and do not in any way amount to proof.

Engelmann, while admitting the essential similarity between 'rigor' and contraction, finds it impossible to explain the former as a thermo-dynamic effect, and falls back on his old imbibition hypothesis.

If there be any truth in the view of so many observers that the wing-fibril of insects is a membranous tubule (a view which I have endeavoured to extend to other muscles), it is difficult to understand to which parts of them Engelmann would attribute the rise of temperature of many degrees, which he is bound to assume. For since each sarcomere is contractile and takes part in a general contraction, he must suppose that some minute fraction of the substance of each sarcomere is the part which suffers the increase of temperature.

Verworn's Hypothesis.

Verworn, in his work entitled *Die Bewegung der lebendigen Substanz* (1892), claims to give a physical explanation of the contraction of muscle by suggesting, by a chain of argument which it is needless to examine, an analogy between it and the retraction of the pseudopodium of an amœba. He regards both the protrusion and the retraction of the pseudopodium as cases of positive 'chemiotaxis' or 'chemiotropism.' Of the protrusion he offers a physical explanation which may be summed up as follows:—The substance of the resting cell has an affinity for oxygen. In a medium devoid of oxygen, its surface becomes spherical through surface-tension. In a liquid medium containing oxygen, molecules of the latter will chemically attract molecules of the cell substance lying at the surface of the cell, and the attraction will be greater at some points than at others. At the former points the molecules of the surface will move to meet the molecules of oxygen in the medium. At each of these

points, therefore, the surface expands; the molecules from within having unsatisfied affinities for oxygen, must take up a position at this part of the surface, and be in turn attracted towards the oxygen of the medium, and so the protrusion increases and a pseudopodium is formed. Retraction he would explain as the result of an alteration of the chemical nature of the molecules at the surface of a pseudopodium, the alteration being the result of stimulation, and of such a nature that the new substance is attracted by substances—the ‘Kernstoffe’—formed by the nucleus and distributed through the cell body with diminishing density from the nucleus outwards. He implies that there is thus produced by stimulation, conditions the exact reverse of those which determined the protrusion of the pseudopodium, but does not attempt to work out the molecular process in detail as before. If we accept as plausible his explanation of protrusion, and attempt to work out the corresponding molecular process to which he attributes the retraction, using his own methods of treating of the molecules and their chemical affinities, we find that it cannot be done. Thus on stimulation, molecules at the surface acquire an affinity for molecules of ‘Kernstoffe’ lying immediately below the surface, and pass towards them in virtue of chemical attraction. We may even suppose that being still unsatisfied by the layer of ‘Kernstoffe’ immediately next to the surface, they proceed still further inwards in search of more ‘Kernstoffe.’ But before they have proceeded more than an infinitesimal distance, they must form a barrier of inert substance between the surface molecules and any ‘Kernstoffe’ within the cell, and so the process must come to an end. However the argument be varied, it does not seem possible to explain retraction on these lines; and Verworn’s explanation of muscular contraction simply consists of a very much forced analogy drawn between it and the retraction of the pseudopodium.

Verworn’s hypothesis as to the causes of retraction of a pseudopodium may perhaps be radically modified by supposing that retraction is due simply to the cessation of those processes which cause protraction, surface-tension alone bringing about the retraction. But when so modified, the hypothesis no longer finds support in the observations on the retraction of pseudo-

podia following stimulation, and on the relations of the nucleus to the cell body, which are the mainstay of the hypothesis in its original form.

In the article referred to above, I pointed out that any increase in the volume of the fluid contents of a sarcomere must tend to cause its side walls to bulge outwards and its ends to be drawn together, and the whole sarcomere to go through just such a series of changes in shape as I have described as occurring during contraction. I accordingly formulated my hypothesis of the processes involved in contraction as follows:—Contraction is the result of an increase in the volume of the fluid contents of the sarcomere, and relaxation is accompanied by a diminution in their volume. I also showed that in the dead sarcomere an increase in the volume of its contents is an efficient cause of shortening. I wish now to record certain observations that make it seem highly probable that in the living sarcomere such an increase in the volume of its contents is not only an efficient cause of shortening, but also the actual cause of normal contraction.

The observations to which I refer were made on isolated sarcostyles of the wing muscles of the house-fly, on fibres from the leg muscles of the water-beetle, and on fibres from the claw muscles of the crayfish, subjected to the action of saline solutions of various degrees of concentration, of distilled water, and of weak lactic acid. They were begun in the hope of producing a contraction of the isolated sarcostyles by the action of distilled water; for I believe that the rigor that is produced in frog's muscle by the action on it of distilled water is a purely physical phenomenon, due to increase in volume of the fluid contents of the sarcomeres by endosmosis from the sarcoplasm.

If sarcostyles be teased out in distilled water from the wing muscles of the house-fly, they are generally found to be fully extended, and they show no marked swelling, though appearing a little turgid when compared with others teased out in normal saline solution. This failure of distilled water to produce either contraction or marked swelling does not mean that distilled water does not tend to cause distension of the sarcomere by osmosis. For, as I have said, the sarcomeres appear turgid (*b*, fig. 1) as compared with others in normal saline solution

(a, fig. 1); and if they are soaked for some minutes in 2 per cent. NaCl solution, and this solution is then replaced by distilled water, they swell rapidly to more than twice their normal diameter, while remaining of the same length. The failure is rather due to the fact that the fluid or viscid contents of the sarcomeres very

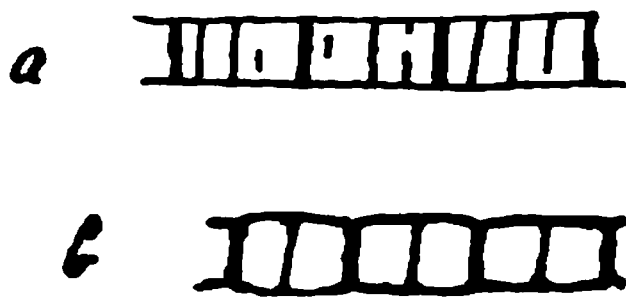


FIG. 1.

rapidly sets or coagulates when the fibrils are exposed to any abnormal influences. Swelling of the contents of the sarcomere cannot, then, take place unless its side walls or its end discs *a* become stretched, and for this the osmotic pressure produced by the action of water on normal sarcostyles seems insufficient. But if the osmotic pressure is made greater by soaking the fibrils in 2 per cent. NaCl solution before putting them into water, the *a* discs yield to the distending force and swelling takes place, the whole fibril increasing uniformly in diameter (fig. 2).



FIG. 2.

Weak solutions of acids cause swelling of isolated fibrils, and a .2 per cent. solution of acetic acid will occasionally cause a very rapid shortening, followed by great swelling and dissolution. But it is very rare to see any marked contraction preceding or accompanying the swelling. Nevertheless, a study of the effects of very weak solutions of lactic acid is instructive. Fibrils are teased out in .7 per cent. NaCl solution, which is then replaced by saline solutions containing .7 per cent. NaCl and various amounts of lactic acid. The weakest solution of lactic acid that I have observed to cause swelling of quite freshly separated fibrils is one containing one part of the strong commercial lactic acid in ten thousand of water. With acid of this strength the sarcomeres usually assume a barrel shape (see fig. 3), with slight shortening, and no yielding of the *a* discs. If they are not quite freshly separated, but have been lying in saline solution for some minutes, acid of this strength produces no swelling, but



FIG. 3.

rather stronger acid (4 parts in 10,000) will cause a rapid swelling, with yielding of the α discs. The degree to which the discs exert any constricting action in such swollen fibrils is very variable. In some cases no constrictions are visible, and the



FIG. 4.

whole fibril forms an even cylinder 4 or 5 m. in diameter (α , fig. 1). But usually both the α and β discs cause well-marked constrictions, and the γ discs are usually visible, and sometimes cause slight constrictions (fig. 4). By washing fibrils in this condition with saline solution they may be made to shrink rapidly to their normal proportions. But after undergoing this swelling and subsequent shrinkage they no longer appear quite normal: the α discs are a little irregular and ragged in appearance, and the whole fibril distinctly presents the appearance of having been overstrained. If fibrils be teased out in distilled water and then swollen by the action of .03 per cent. lactic acid, they may be made to shrink again by washing them with water, just as by washing with saline solution in the preceding experiment.

By using slightly stronger acid the normally inextensible side walls of the sarcomeres may be stretched in the same way as the α discs. Each sarcomere then appears of its normal shape, but all its measurements are approximately doubled. Still stronger solutions of acid cause very rapid swelling and dissolution.

The exact nature of the chemical or physical process involved in this swelling of the sarcomere under the action of dilute acids is not clear. The process is perhaps analogous to the swelling of fibrine filaments when immersed in weak acid. But it is clear that the presence of extremely dilute lactic acid may cause a very rapid passage of a large quantity of water into the sarcomeres. And it is also clear from these observations that distilled water tends to pass into the sarcomeres by osmosis.

I have said that it is unusual to see more than a very slight degree of shortening produced in isolated wing fibrils by these agents that tend to cause distension of the sarcomeres, and I believe that this is due to the fixation or coagulation of the contents of the sarcomeres by their immersion in these abnormal

fluids. This statement is justified by a study of the behaviour of fibrils teased out in white of egg, and in white of egg mixed with equal quantities of saline solutions of various degrees of concentration. If fibres from the wing muscles of the house-fly be teased in either white of egg or a mixture of equal parts of white of egg and .7 per cent. NaCl solution and examined at once, numerous fibrils are seen contracting rapidly: and after about thirty seconds all the fibrils, many of which were at first almost completely extended, appear fully contracted. White of egg is said by Hammarsten to contain about .7 per cent. of mineral salts. If, therefore, it is mixed with an equal quantity of 5 per cent. NaCl solution, the mixture will contain about 2.8 per cent. of mineral salts. Fibrils teased out in such a mixture usually remain fully extended.

White of egg with an equal quantity of 2 per cent. NaCl solution is a mixture containing about 1.3 per cent. of salts. When fibrils are teased out in this mixture they usually contract to some extent, but slowly; and many contract only partially. If fibres be allowed to lie in this mixture for five or ten minutes before the fibrils are teased out, it is usual for all the latter to remain completely extended, though some may contract slightly. If isolated fibrils be allowed to soak for some time in these mixtures containing much salt, many of them soon show a distinctly collapsed appearance, i.e., the sarcomeres have their side walls partially sunken inwards, so that they now seem no longer fully distended, but shrunken.

A mixture of white of egg and 1 per cent. NaCl solution contains about .85 per cent. of salts. Fibrils teased out in this mixture contract well and uniformly, but if the fibres be allowed to soak for ten minutes in the mixture before the fibrils are teased out, contraction is much retarded and very imperfect in most cases, while a preliminary soaking for fifteen minutes is usually enough to prevent contraction entirely.

A mixture of white of egg and distilled water contains about .35 per cent. of salts. Fibrils teased out in this mixture always contract rapidly and completely, and do so, even if the fibres have been soaked for half an hour or more in the mixture.

These results are readily explicable in terms of the working hypothesis of contraction that I have suggested. The sar-

comeres of the teased-out fibrils are in such a condition of distension that when they are subject to no extending force they remain contracted. Those which are isolated by teasing are necessarily drawn out in the process of being ruptured across. They then rapidly resume the condition of retraction or contraction so long as the medium in which they lie is one which does not materially alter their physical state. White of egg mixed with normal saline solution is such a medium. But if the mixture contains a large proportion of salts, there is caused a passage of fluid out of the sarcomeres (as proved by the conditions of partial collapse produced by the long continued action of the fluid), and this relieving their condition of tension or distension, removes thereby their tendency to contract. On the other hand, the mixture of white of egg with water probably causes a passage of fluid into the sarcomeres, and so, by still further distending them, increases their tendency to contract.

This interpretation of the facts is fully borne out by a study of the effects of similar agents on fibres from the leg muscles of the water-beetle and from the claw muscles of the crayfish. Fibres of the former kind, when separated with needles in .75 per cent. NaCl solution, if not at first in a state of complete contraction, usually contract slowly to the maximal extent. If the saline solution be replaced by distilled water, contraction proceeds more rapidly and certainly. If the muscles be soaked for ten to fifteen minutes in a 2 per cent. NaCl solution and then separated in this same solution, most of them are found in a state of complete extension, and remain so. If, then, the 2 per cent. NaCl solution be replaced by one containing only 1 per cent. NaCl, in the first few seconds there is no apparent result, but usually after about ten seconds a slow contraction begins, and then, growing more rapid, continues until all the fibres are wholly contracted. If a 1 per cent. NaCl solution fails to produce this result, one containing .75 per cent. NaCl will invariably do so. When weaker solutions are used, contraction begins and proceeds more rapidly, and most rapidly when distilled water is used. When a slow contraction set up by a 1 per cent. solution has begun, it may sometimes be stopped by swilling the fibre with a 2 per cent. NaCl solution.

Assuming that my account of the structure of these fibres be the true one, *i.e.*, that their muscle columns are similar in all essential respects to the cylindrical sarcostyles of the insect's wing muscles, these facts are readily explicable on the same lines as those just dealt with. The sarcomeres are in a condition of chronic distension, *i.e.*, they have tone, and when separated in an inert fluid they contract. When they are separated in distilled water, water passes by osmosis into the sarcoplasm, and thence into the sarcomeres also, so increasing their distension, and causing a more rapid and powerful contraction. When they are soaked in 2 per cent. NaCl solution, water passes from the sarcoplasm, and therefore also from the sarcomeres; the condition of distension of the sarcomeres is removed, and therefore the tendency to spontaneous contraction. When 1 per cent. NaCl solution is added, it acts on the fibres containing a raised percentage of salts just as pure water acts upon normal fibres,—it produces, in fact, a water-rigor.

In just the same way, a 1 per cent. NaCl solution will abolish the tendency to spontaneous contraction, though less rapidly and certainly than does the 2 per cent. solution. Contraction may then be produced by means of .75 per cent. solution, but much more certainly by .5 per cent. solution. This seems to be explicable in just the same way as the previous case.

If to fibres lying relaxed in 1 per cent. NaCl solution there be added a solution containing 1 per cent. NaCl and .03 per cent. lactic acid, a contraction results after a few seconds, which is quite similar to that produced by distilled water. Now we have seen that a still weaker solution of acid than this will cause a very rapid passage of large quantities of fluid into sarcomeres of isolated sarcostyles, and it seems highly probable that the acid causes contraction in this case by leading to the passage of fluid into the sarcomeres, just as pure water and weak saline solutions seem to do.

Since the contractile elements of the claw muscles of the crayfish are unquestionably cylindrical sarcostyles exactly similar to those of the insect's wing muscles, it seemed worth while to repeat this last series of experiments on them. Water and saline solutions seem to exert on these muscles a very rapidly injurious effect; and when pinned out with their

natural attachments in the extended state, the fibres have so strong a tendency to contract that they usually break away from their attachments, and contract completely. But after being soaked in mixtures of white of egg and saline solution in equal parts containing 2 per cent. of salts, they may be obtained in a fully extended or relaxed condition. The addition of weaker saline solutions or water then causes contraction, which is rapid and certain according as there is a low percentage of salts. In a similar way, a mixture of white of egg and saline solution containing 1 per cent. of salts will cause a condition of complete relaxation; and fibres in this state contract on the addition of .5 per cent. of NaCl solution or 1 per cent. NaCl solution containing .03 per cent. lactic acid. In my previous paper I pointed out how, in regard to structure, these muscles form a natural link between the types of the wing muscles and the leg muscles of insects, and we see here that in these respects also they are intermediate in character to those two types of muscle.

My interpretation of these results finds further support in certain observations made by Mr W. M. Fletcher of Trinity College, which he has not yet published. He has most kindly given me permission to make use of such of his results as throw most light on the problem in hand. It has long been known that frog's muscle, when immersed in distilled water, or when water is pumped through its vessels, passes into a long continued state of contraction, and that this state of contraction may be abolished by immersing the muscle in 2 per cent. NaCl solution, or pumping this solution through its vessels. In the course of a series of very delicate estimations of the amounts of carbonic acid given off from surviving muscles in units of time at various periods after excision from the body, Mr Fletcher has found that when a frog's muscle passes into a well-marked water-rigor owing to immersion in distilled water, there is no increase in the rate at which CO_2 is being given off from the muscle at the time. This observation, although not conclusive, would seem to indicate that the water does not produce its effect by causing a chemical change in the same way as ordinary stimuli, but that its effect is rather a purely physical one. It therefore lends support to the explanation of water-rigor that I have suggested,

namely, that it is due to the passage of fluid into the sarcomeres, owing to a reduction of the osmotic equivalent of the fluids of the sarcoplasm.

Mr Fletcher has also shown that when a muscle is immersed in a weak solution of lactic acid (4 parts of acid in 10,000 of normal saline solution), a well-marked contraction rapidly ensues and persists. And, just as the water-rigor may be abolished by immersion of the muscle in 2 per cent. salt solution, so this acid-rigor may be slowly abolished, at least in part, by immersion in normal saline solution. Now, I have shown that acid of less concentration than this (namely, 1 part in 10,000) will cause swelling of isolated sarcostyles, even when they are already partially altered and set by immersion in saline solution: and that by washing with saline solution free from acid, the swelling may be as rapidly abolished. It seems, then, probable that the weak acid produces its effect on the whole muscle by causing the passage of fluid into the sarcomeres, and that the relaxation of the muscle on subsequent immersion in normal saline solution is due to a washing away of the acid. It is true that Mr Fletcher finds that the immersion of the muscle in the acid and the onset of the acid-rigor is accompanied by a sudden increase in the amount of CO_2 given off by the muscle. But there are good reasons for believing that the sarcoplasm of the muscle contains a certain amount of CO_2 in a state of loose chemical combination; and it is highly probable that the increase in the amount of CO_2 given off may represent this stock of loosely combined CO_2 suddenly set free by the advent of the acid.

In my previous paper I suggested that contraction is due to a passage of water from the sarcoplasm into the sarcomeres, owing to an increase in the osmotic equivalent of their contents; and that this increase is due to the splitting up of large unstable molecules into a larger number of smaller molecules. The observations recorded above form a basis for further speculation on the cause of contraction, and suggest that, while an increase in the number of molecules in solution in the sarcomeres may be in part the cause of passage of fluid into them, probably a more important factor in bringing about the result is the presence of lactic acid among those newly formed molecules. There

are reasons for believing that if lactic acid is the main agent in the process, it is produced in the sarcomeres rather than in the sarcoplasm. The experiments mentioned above, in which isolated sarcostyles were swollen with acid, and subsequently made to shrink by washing with saline solution or water free from acid, indicate that it is the presence of acid in the contents of the sarcomeres that determines the taking up of water and the holding of it by those contents. In making these experiments with acids, I have frequently noticed that the immediate effect of adding a solution of acid, too weak to cause a swelling of the fibrils, is to cause a well-marked sudden shrinkage of them. There seems to be a passage of fluid out of the sarcomeres, caused by the presence outside them of acid which has not yet permeated their substance.

In those experiments in which a solution containing .01 per cent. lactic acid caused the passage of a large quantity of water into the sarcomeres of isolated sarcostyles, the latter had been lying in saline solution, and were already partly set or coagulated, and less easily affected by the acid than quite unaltered sarcostyles would be. This alteration is proved by the fact that sarcostyles only partially teased out from the fibres, *i.e.*, lying still embedded in sarcoplasm, and therefore less affected by the saline solution, are generally swollen by weaker solutions of acid than those that are lying free in the fluid. It seems probable, then, that the setting free of a very minute quantity of lactic acid in the chambers of the normal living sarcomere is sufficient to cause the passage into the sarcomere of a quantity of fluid. It would seem probable, therefore, that the production of so small a quantity of acid as would constitute the contents of the sarcomere a .001 per cent. solution, or even of a still smaller quantity, may cause the passage into the sarcomere of enough fluid to bring about contraction.

I would suggest, then, that contraction is the result of the passage of fluid into the sarcomeres from the sarcoplasm, determined by the setting free of lactic acid in the fluid contents of the sarcomere, aided perhaps by an increase in the osmotic equivalent of these fluid contents through an increase in the number of molecules in solution. Then, so long as the acid remains present in the fluid of the sarcomere, the additional fluid absorbed

will be retained and the state of contraction will continue. But as soon as the acid escapes from the sarcomere, the additional fluid will also escape with it into the sarcoplasm, and allow relaxation to take place, just as in the case of the isolated sarco-styles swollen by acid, rapid shrinkage results from washing out the acid with water, and in the case of acid-rigor, relaxation results from immersion in normal saline solution. It is probable that in normal muscle the sarcoplasm contains a store of alkaline substances specially adapted for taking up the acid of the sarcomeres, and that the acid is no sooner produced than it begins to pass out into the sarcoplasm, either as lactic acid, or perhaps, having undergone a further change, as carbonic acid.

If we adopt this as a working hypothesis of the processes immediately concerned in contraction and relaxation, we can give explanations of many of the well-known phenomena of muscular activity. We see that relaxation is, in a sense, an active process, for it does not depend merely upon the cessation of some change causing contraction, but is the result of a distinct physical process, namely, the escape of fluid from the sarcomeres. Many considerations have led physiologists to the conclusion that relaxation is in fact an active process.

The form of the curve of simple contraction may be explained thus:—The sudden production of acid leads to an inrush of fluid into the sarcomeres, which is most rapid at first, and becomes slower as the acid escapes, until the amount of acid present is no longer enough to hold this additional fluid in the sarcomeres. The additional fluid then begins to escape, most rapidly at first, then more slowly, since the acid must escape most rapidly when it is present in largest quantity, and very slowly when most of it has already escaped. Hence the long drawn-out character of the lowest part of the curve of relaxation.

It is well known that the first part of a contraction is the most forcible, and that three small contractions give a larger proportion of work to heat than one large one that does the same amount of external work as the three together (I., s. 167). The action of the elastic discs of the sarcomeres must tend to produce just this result, for in a large contraction there must be a greater proportion of the whole transformed energy spent in doing work in stretching the elastic discs in the later than in

the earlier stages of contraction, and this part will appear not as external work, but as internal heat. Hence the greater economy of small contractions as compared with large ones. Probably other factors besides play a part in determining the greater force of the early part of a contraction. Thus, if the setting free of acid in the sarcomeres is very sudden, practically instantaneous, there will be developed a certain hunger for water, or power of attracting water, which becomes feebler as it becomes more and more satisfied in the earlier stages of contraction. It seems probable also, from a consideration of the conditions, that the distending force must act on the walls of the sarcomeres at a greater mechanical advantage in the early than in the later stages of contraction.

The facts of summation of stimuli are very fully explicable in terms of this hypothesis. When a second stimulus is thrown into a muscle before the contraction due to a former stimulus of the same strength has passed away, the second contraction rises from that point on the curve of the first contraction at which it is thrown in, as from a new base line, but does not rise quite so high as it would from the normal base line (II., p. 117). Thus, in fig. 5 (copied from Helmholtz), if the second stimulus be thrown in at *b*, the second contraction rises almost to an equal height with the first one. For at the point of time *b*, the sarcomeres of the muscle are distended with the whole of the additional fluid that has passed in as the result of the setting free of acid at the point *a*, while the acid itself has mostly escaped, so that it can no longer hold this additional fluid in the sarcomeres. When at this point, *b*, a second quantity of acid equal to the first is set free, the escape of the additional fluid already present is prevented, and the entrance of a second quantity equal to the first is determined. But, as we have already seen reason to believe, the distending force acts at less advantage when the sarcomeres are already partially contracted, and so the second rise is not quite so high as the former one. Just in the same way, when a second stimulus is thrown in at any point on the descending part of the curve, the further escape of the additional fluid is arrested, and the entrance of a second quantity is determined, and the contraction rises to a height corresponding to the sum of these two quantities of addi-

tional fluid. When the second stimulus is thrown in at a point on the ascending part of the curve of the former contraction (g in fig. 5), the acid set free at that point begins to escape in the same way as that liberated by the former stimulus; and so, after an interval $g-h$, equal to the interval $a b$, it has diminished in quantity to the point at which it can no longer hold the additional fluid. The height of the contraction therefore represents the amount of fluid that passes in during the time $a h$. The curve of relaxation we may regard as consisting of the two parts $h i$ and $i k$, the former representing the escape of the additional fluid that has passed in during the period $g h$, the latter that of the fluid that passed in during the period $a g$.

The contraction resulting from the summation of two or more stimuli, each of which alone is subliminal, such as occurs in

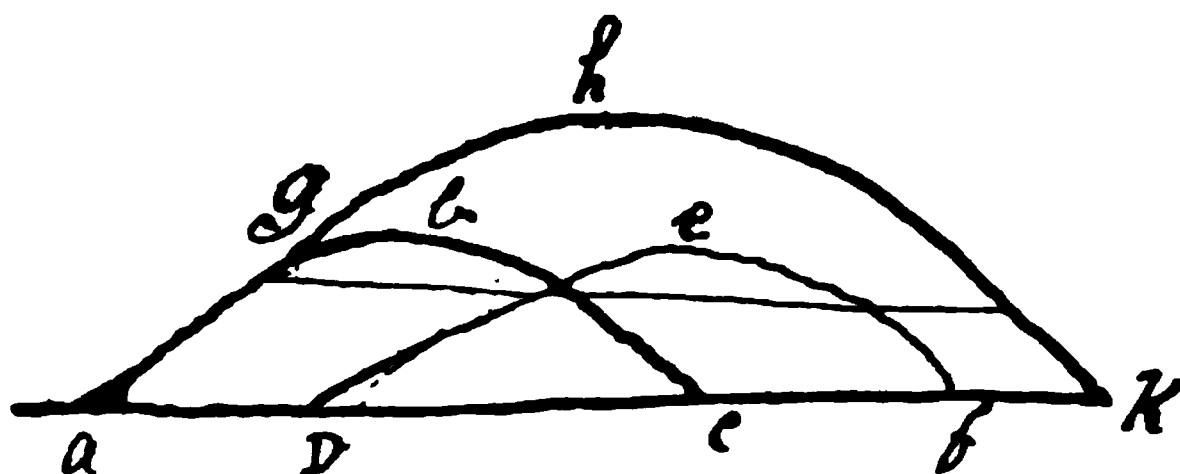


FIG. 5.

crab's muscle (II., p. 117), demands a different explanation. It must be supposed that the acid set free by the first stimulus is insufficient to cause a flow of fluid into the sarcomeres, but that when a second stimulus follows after the first before the acid liberated by the first has had time wholly to escape, then the percentage of acid in the sarcomeres is large enough to cause the inflow of fluid, and contraction results.

There is a group of phenomena—the staircase, fatigue in excised muscles, the effects of deprivation of circulation, etc.—which seem to be all explicable by means of one not improbable assumption. I have said that the sarcoplasm probably contains a stock of alkaline substances which, in a fresh muscle, are hungry for the acid products of the sarcomeres, and that after contraction they take up the acids, probably in the form of carbonic acid, and pass them on to the lymph and blood. That

there is some such storage of CO_2 is made almost certain by the observation by Mr Fletcher of the fact that a simple contraction or a few simple contractions do not cause any increase in the amount of CO_2 that is being given off by an excised muscle, while immersion in very dilute acid does cause the giving off of an increased quantity of CO_2 during the first few minutes. It is clear that if relaxation depends upon the escape of the acids, and this escape depends, as it must, upon the state of the sarcoplasm, then in an excised muscle, on repeated contraction, the alkalinity of the sarcoplasm must diminish, its hunger for the acids must be partially satisfied, and the acids will then escape from the sarcomeres less rapidly. We see here, then, the explanation of the lengthening of the curve of relaxation through fatigue in excised muscles, while the curve of shortening remains unaltered. The cutting off the circulation through the vessels of a muscle is said to affect the curve of its contraction in just the same way, and a similar explanation seems to apply to this case. The slow metabolism of the resting muscle, on which its tone may be supposed to depend, must lead, in the absence of the circulation, to a partial saturation of the sarcoplasm with the waste products of the sarcomeres. The acids will then no longer escape from the sarcomeres so rapidly as in a muscle from which the circulating blood continually carries the CO_2 and other waste products away from the sarcoplasm.

Fatigue of this kind may be in some degree removed by the circulation of a simple saline solution (which presumably acts by washing out the acid waste products), and Ranke has shown that by injecting an extract of fatigued muscle, fatigue symptoms may be produced. He has further shown that the active substances concerned are CO_2 , lactic acid, and acid sodium phosphate; and Hermann has pointed out that other acids will produce similar symptoms, and that weak alkalies will remove these symptoms (I., s. 23). When a muscle with intact circulation is repeatedly stimulated, fatigue is manifested by a diminution of the height of the curve of contraction: it may in this case, perhaps, be regarded as chiefly due to a using up of the reserve substances on whose metabolism contraction depends. But all the facts quoted above support my suggestion that the fatigue symptoms of excised muscle are due to the accumulation

of acids in the sarcoplasm of the muscle. My hypothesis then explains the 'modus operandi' of this accumulated acid and brings together, as effects of this one cause, a long series of phenomena, the relations between which have hitherto been quite obscure. For assuming, as we have seen reason for doing, that the rapidity of escape of acid from the sarcomeres depends upon the capacity of the sarcoplasm to take it up readily and that this capacity, in turn, depends upon the presence of a certain store of alkaline substance in the sarcoplasm then it is clear how the accumulation of acid in the sarcoplasm must diminish its capacity for taking up more acid, and so make the escape of acid from the sarcomeres less rapid.

We may now apply this conception of the processes underlying the fatigue of excised muscle to the detailed explanation of a series of phenomena. And we may begin by a mention of the 'verkürzung-rückstand.' When a muscle is weighted with a very small load, the curve of its contraction returns to the base line only very slowly. This long continued slight degree of contraction is what Hermann has called the 'verkürzung-rückstand.' When an excised muscle has been made to contract several times in rapid succession, the amount of this residual contraction is much greater and persists much longer and is called 'contracture' (I., § 23).¹ The 'verkürzung-rückstand' may be explained by supposing that the rate of escape of the acid from the sarcomeres during relaxation progressively diminishes, so that the last quantities escape only very slowly, and so a part of the additional fluid absorbed by the sarcomeres during contraction escapes only very slowly also.

Then, in an excised muscle the acid taken up by the sarcoplasm in a first contraction does not escape from it, and the readiness of the sarcoplasm to take up more acid is thereby diminished. The acid causing a second contraction therefore escapes less rapidly than that which caused the first one, and the 'verkürzungs-rückstand' is therefore larger. And with each succeeding contraction the readiness with which the sarcoplasm will take up more acid is diminished, and the escape of acid from the sarcomeres is therefore less rapid and the

¹ Biedermann uses this word in another sense.

'verkürzungs-rückstand' greater, until it is so marked as to deserve the name 'contracture.'

The phenomenon of the 'staircase' seems to be another effect of this accumulation of acid in the sarcoplasm, and consequent slower escape of acid and water from the sarcomeres. The curve of fig. 6 illustrates this phenomenon in the case of an excised frog's muscle. Each contraction in a closely following series is higher than the immediately preceding contraction, and after a short interval the first contraction of a second series is lower than the last, but higher than the first, of the former series. In each series, each contraction leaves in the sarcomeres a certain residuum of acid and additional water which determine the 'verkürzungs-rückstand.' And each contraction leaves the sarcoplasm less ready to take up more acid: the escape of acid in each contraction will therefore be less rapid than in the preceding contraction, and the residual amount in the sarcomeres will be greater. Each contraction-curve will therefore start

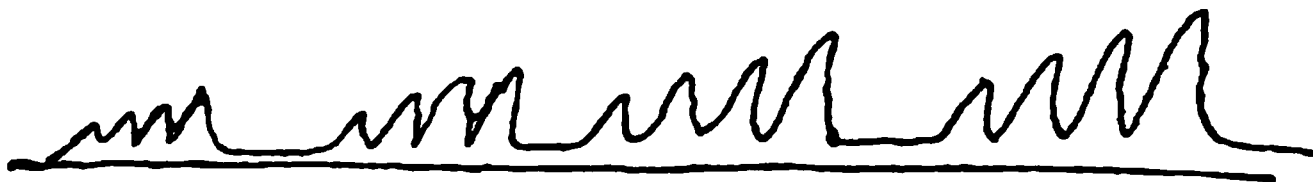


FIG. 6.

from a higher base line, and in so far will tend to be higher than its predecessor. But there is another factor tending towards the same end. Since the escape of acid from the sarcomeres is slower, a longer time must elapse after the point at which the acid was set free before the quantity of it in the sarcomeres is insufficient to attract more water. The passage of water into the sarcomeres will therefore continue for a longer period, the amount that passes in must be greater, and therefore the curve of contraction must be higher.

In exactly the same way, we may explain the fact that a stimulus will cause a higher rise of the contraction-curve after a short tetanus than one of the same strength thrown in before the tetanus.

Tetanus results when stimuli follow one another at such a rate that each one arrives before the contraction caused by the preceding one has passed away. A 'staircase' series of contractions may be regarded as the most incomplete form of

tetanus. In a complete tetanus, the contraction-curve rises higher than that of a simple contraction due to the most powerful stimulus, and there are no oscillations of the curve. We must suppose that each succeeding stimulus sets free a fresh quantity of acid in the sarcomeres, while the acid of the preceding stimulus is still causing an inrush of fluid. There is therefore maintained such a degree of acidity of the contents of the sarcomeres as will tend to cause a constant inflow of fluid; and when a maximal contraction is reached, will determine its persistence. "The height of the tetanus-curve grows with the strength of excitation, or, where this is constant, with its frequency. The steepness of the rise alters in the same proportions" (II., p. 121); for, with increased strength or frequency of excitation, the degree of acidity of the contents of the sarcomeres must be maintained at a higher level.

It seems impossible to draw any sharp line between 'contracture' and natural 'rigor.' For if an excised muscle, whose circulation has been cut off, be repeatedly tetanised, the curve of relaxation becomes more and more prolonged, until there is no perceptible relaxation, and this condition seems to pass imperceptibly into 'rigor.' I would therefore regard natural 'rigor' as an extreme state of fatigue, and as due to the same cause as the prolongation of the curve of relaxation in the fatigue of excised muscle, namely, the accumulation of acid in the sarcoplasm. We must suppose that in an excised muscle metabolism continues at a slow rate. The waste products must then accumulate in the sarcoplasm, and sooner or later a time must come at which the capacity of the sarcoplasm for taking up and fixing more acid is abolished. If the slow metabolism in the sarcomeres then continues, the acid produced must accumulate in the sarcomeres, and will then reach such a degree of concentration as results from a stimulus applied to the muscle. Fluid will then pass into the sarcomeres from the sarcoplasm and cause contraction; and since there is no way of escape for the acid, this additional fluid will remain in the sarcomeres, and the state of contraction will persist. In a late stage of 'rigor mortis' there is probably a much more profound alteration of the chemical constitution of the muscle, notably the formation of myosin; but that there is no such change in

the early stages of 'rigor mortis' is indicated by the fact that it may be abolished by the circulation of serum through the vessels of the muscle (L. s. 146), just as the acid-rigor may be abolished by soaking the muscle in saline solution. That there is no great sudden chemical change accompanying the onset of 'rigor mortis' is indicated by observations made by Mr Fletcher of the rate at which CO_2 is given off by a muscle from the time of its excision till the time of its death. He finds that the curve indicating this rate at successive intervals of time after excision has very constantly some such form as that in fig. 7. I must pass without discussion the interesting features of the first part of this curve, and merely state that the contraction of 'rigor mortis' occurs at a time corresponding to some part of the level plateau, and that there occurs at this time no increase



FIG. 7.

in the rate of escape of CO_2 . These observations, therefore, support very strongly my view of the nature of the contraction of 'rigor mortis,' for they indicate the continuance of a constant slow chemical change of a nature similar to normal metabolism, and the occurrence of contraction when this change has continued for a certain time. The contraction would therefore seem to be an effect of the accumulation of the products of the slow chemical change. The 'modus operandi' of those accumulated products I have already suggested.

This view of the nature of the early stage of 'rigor mortis' is further borne out by the fact that heat, and everything that favours a rapid metabolism, hastens the onset of 'rigor,' while cold delays it, and that previous fatigue also powerfully favours the rapid onset of 'rigor'; for these are factors that tend to cause an accumulation of acids in the muscle.

The nature of water-rigor and the process of its abolition by means of 2 per cent. NaCl solution I have already discussed, and have indicated my view of the processes concerned.

The view here adopted of the influence on contraction of the waste products of metabolism finds confirmation in the fact that those muscles of which very rapidly succeeding distinct contractions are required, contain a relatively very large amount of sarcoplasm, and elaborate arrangements for carrying off the waste products of metabolism. Thus the insect's wing muscle has a very large amount of sarcoplasm which is permeated in all its parts with a very dense network of fine air-tubes. These tubes constitute a very perfect system for carrying carbonic acid away from the sarcoplasm. So also the fibres of the muscles of the bat's wing contain a very large amount of sarcoplasm, and are very slender; and each one of these slender fibres is surrounded by an extraordinarily dense network of capillary blood-vessels.

It is generally agreed that a satisfactory theory of muscular contraction must be capable of affording explanations not only of the contraction of striated muscle, but also of that of plain muscle fibres, and of the movements of cilia and amoeboid protoplasm.

I do not at present see how my theory of contraction can be applied to the explanation of the contraction of plain muscle, and I am inclined to believe that this is due to our ignorance of some definite structure that exists in these fibres. There has been described a regular transverse striation in muscle fibres classed as smooth, and I have been able to make out indications of transverse markings in the fibres of the frog's bladder, by the application of Rollett's negative gold staining process. But, hitherto, I have endeavoured in vain to obtain more evidence of definite structure in plain muscle.

The movement of cilia may possibly be explained as the result of just such a process as I have suggested to be the cause of muscular contraction. If, as Schaefer has suggested,¹ a cilium is a hollow tubule, of whose wall one side is more easily extensible than the other, and if the cavity of this tubule is shut off by a permeable membrane from the general cell substance, then

¹ *Proc. Roy. Soc*, vol. xlix.

we may suppose that the bending of the cilium is the result of the sudden production of acid in the contents of the tubule, and the consequent passage of fluid into the tubule from the general cell substance; for such an inflow of fluid in distending the cavity would cause an extension of the more extensible side of the wall of the tubule, and therefore a bending of the tubule towards the opposite side. The water-rigor of cilia would also be explicable on just the same lines as that of muscle.

To extend this theory of contraction to the explanation of protoplasmic movement is a task that seems full of difficulty, yet I think that Bütschli's demonstration of the existence of alveolar structure in so many different kinds of protoplasm affords an indication of the lines along which the explanation is to be sought. If any part of the protoplasm of an amoeba is similar in constitution to the contents of the sarcomeres of muscle, then the setting free of minute quantities of acid in those parts would be an efficient cause of movement of fluid towards that part. It may be that, on stimulation of some spot on the surface of a lobose pseudopodium of the amoeba, acid is set free by chemical decomposition in the substances occupying the alveoli of that part, and that these then exert so strong an attraction for the fluids of the cell body that the whole cell flows towards the stimulated part, so that the pseudopodium becomes retracted.

In the linear series of alveoli that Bütschli has described in the contractile threads of certain infusoria, we may perhaps see the first step in the evolution of the cylindrical sarcostyle.

In concluding, I wish to thank Mr W. M. Fletcher very heartily for permission to make use of his unpublished observations.

ANOMALOUS FEMALE URO-GENITAL ORGANS. By
N. BISHOP HARMAN, B.A., St John's College, M.R.C.S.
(Eng.), &c., *Demonstrator of Anatomy, Cambridge University.*
(PLATE V.).

THE following is a description, with some remarks, on anomalies of unusual character found in a female subject æt. 9 months. The child was admitted to Addenbrooke's Hospital, Cambridge, 7th August, suffering from rickets and general malnutrition, and died the following day, after a series of convulsions of no definite character. An autopsy was conducted by Professor Kanthack, to whose kindness I am indebted for the opportunity of making a detailed examination of the internal organs, which were removed from the body with some lumbar vertebræ. Dr Kanthack reports that the examination of the external parts revealed no anomalous conditions, and that the vulva, as regards its superficies, appeared quite natural. Further examination revealed quite a different condition of the internal organs, which showed the following peculiarities.

The sketch (Pl. V. fig. 1) shows that on the right side of the body the usual generative apparatus—tube, ovary, etc.—with the kidney, are developed, though these, in position, size, and shape, differ from the average; whilst on the left side a long fusiform body, in colour and consistency like to that of the right sex-gland, is, save for a small tuft surmounting the anomalous sex-gland, the only representation of the left uro-genital apparatus.

The single kidney of the right side (fig. 2) is of large size (weight 25 grammes) and irregular shape, lobular in the usual manner of such young organs, but presenting no resemblance to the common shape, being roughly pyramidal,—a broad dorsal surface is in relation to diaphragm, and abdominal parietes extending as far posteriorly (caudally) as the iliac crest. Ventrally it presents two surfaces: an anterior (cephalad) in relation to the right lobe of the liver, which organ presents

a correspondingly enlarged 'renal impression'; and a posterior (caudal) surface in relation to the colon. A mesial surface presents at its fore part a deep sulcus, in place of the usual hilum, which is guarded by two thick lips of renal tissue, between which the vessels and ureter penetrate for about 15 mm. to their renal connexions.

Section of the kidney shows that its papillæ radiate in almost all directions from a common centre—the pelvis uretralis, which is very small, the calyces arising almost as branches from the ureter directly.

The ureter presents a singularly convoluted and sacculated arrangement; the bends are united by webs of tough connective tissue. This appearance suggested at first some obstruction near the bladder, but this proved not to be the case, for a stylet, passed through a buttonhole in its mid-length, traversed its length both ways with the greatest ease. Also the child is reported to have passed urine in normal quantities. The length of the tube in the undissected state measured 65 mm., with the bands uniting the bends removed 135 mm. Besides the convolutions, two large sacculi of crescentic shape were present.

At its posterior extremity the ureter passed lateral to the uterus, and entered the bladder by the usual oblique valvular opening, about 1 mm. to the right of the median line.

The bladder, with the exception of its connection with the uterus, is normal in shape, size, and thickness; its urethral opening was, however, large, measuring nearly a centimetre in diameter.

Attached to the right wall of the bladder is a single-horned uterus, which occupies a position quite to the right side of the body, or projects considerably above the pelvic brim, whilst anteriorly its extremity curves gently to the right, and is continued into a well-grown Fallopian tube, lying in the ligamentum latum, and ventral to and parallel with the psoas muscle, the ovary being mesial to the tube.

Section of the uterus shows its cavity to be about 15 mm. in length, and to contain a thick white tenacious mucus; below, its cavity ends blindly and bluntly, the wall joining with that of the bladder, the two becoming insensibly blended, so that section of

the lower part of the right wall of the bladder differs only from that of the left in a barely distinguishable increase in thickness. Thus no vagina exists, and the uterus presents no differentiation into body, cervix, or os.

The ovary, situated mesial to the tube and ventral to the ligamentum latum, is normal in structure; the hilum contains tubules, which indicate the presence of the parovarium. The usual plica gubernatrix is present, and has gained an attachment to the horn of the uterus, thus forming utero-ovarian and round ligaments.

An attempt was made to find glandular remains of the Wolffian body, described by von Recklinghausen as existing in the periphery of the lateral wall of the uterus, to which Freund attributes the origin of his first class of "Adenomyome der Uteruswand" (Bücheranzeigen, *Centralblatt für Pathologie*, vol. vii., p. 302 *et seq.*).

Transverse sections of the single-horned uterus were made, but no trace of such structures could be found, neither were there certain indications of the existence of a duct of Gärtner.

The greatest interest of the specimen, however, centres in the left side. There we find a long or rather fusiform body, presumably a sex-gland, of dead white colour, rising up from the peritoneum of the dorsal parietes, to which it is attached throughout its whole length by a short peritoneal ligament, which is occupied by a dense vascular plexus, causing it to present a dark purple colour. Its length measures 42 mm., its ventral surface is smooth, its edges are notched.

Attached to the anterior extremity of the sex-gland is a tuft of reddish tissue, consisting of some five lobes, some of which are pedunculated.

Passing posteriorly from the sex-gland beneath the peritoneum is a delicate band, which can be seen crossing the median line to reach the uterus; whilst from above passes a plexus of veins, with a single artery, which are continuous with the vessels of the left suprarenal capsule. There was also a second band of tissue (not shown in sketch), which passed anteriorly, at first parallel to the vessels, but diverging from them to reach the diaphragm ventral to the aortic opening.

Examination of these various structures by the microscope

shows that the presumed sex-gland (figs. 3 and 4) is undoubtedly an ovary. The peripheral and central stroma are sharply defined; a few well-developed Graafian follicles with normal contents are seen, though the great majority of the ova have not passed the primitive stage. No tubes of Waldeyer could be found penetrating from the germinal epithelium.

The germinal epithelium is not normal, being nowhere cubical in character: on the ventral surface this might well be accounted for by the handling to which the specimen was subjected, but in the protected dorsal surface the cells are flattened also.

The mesovarium contains a network of vessels, among which, at its anterior part, are a few tubules, like to those figured in the next section.

The minute structure of the reddish tufts surmounting the gland is shown in fig. 5. The lobules consist of a mass of soft fibrous tissue, in which are scattered, usually in clusters, tubules lined by cubical—non-ciliated—epithelium. The lobules present sharply defined cortical and medullary parts: the structure of the parts, however, only differs in that the cortical tissue is denser in texture, or its tubules more compressed. The tubules are by no means numerous. This tuft may be fairly taken to represent an ill-developed Wolffian body.

With regard to the bands anterior and posterior to the sex-gland, the anterior proved to be connective tissue environing a few nerve strands which joined with the solar plexus; some of the fibrous tissue passed on to the diaphragm, but this, in view of the nervous connexion, will hardly allow of the band rising to the status of a *plica gubernatrix superior*.

In the posterior band one hoped to find some relic of a Wolffian or Müllerian duct, of which ducts no other traces could be found, but this hope was destined to be disappointed: the band, very slender anteriorly, but thicker posteriorly, is closely adherent to, and indeed is part of, the fibrous tissue of the peritoneum, being inseparable from it. Microscopical examination shows merely fibroid tissue, with a few blood-vessels.

The asymmetrical condition of the branches of the abdominal aorta (fig. 6) presents some interest in the presence of only one hypogastric artery—that of the left side. The bulb represented

on its extremity was situated at the umbilicus, and proved to be a mucous cyst.

It may also be remarked that both suprarenal capsules are present,—the left, as is frequently found, being the larger.

To comment on the arrangements of the organs of the right side is not difficult—save in one particular. The great size of the kidney is undoubtedly compensatory.

The arrangement of convolutions and sacculation of the ureter is, however, obscure in its causation. The functional patency of the ureter was as certain as the freedom of the passage of the style. That it could not be from past obstruction is evident from the less tortuous anterior end and the smallness of the pelvis uretris; also the longitudinal arrangement of the fibrous strands connecting the bends suggests rather that the shape and great length (135 mm.) of the tube is the result of some hyperplasia, than distortion from obstruction.

The internal genital organs of the right side, as has been shown, are normal—save in their retention of the foetal position.

The absence of the vagina, a by no means uncommon anomaly, is of doubtful significance. It may be due to failure of the Müllerian duct to reach the cloaca.

On the left side the anomalies are of less easy explanation.

Accepting the fact of no traceable remains of Wolffian or Müllerian ducts, may we believe the development of a Wolffian body or sex-gland possible in the absence of such ducts?

In regard to the sex-gland, there seems no difficulty in accepting such a conclusion: the history of its development does not suggest in any way its dependence on the presence of a duct.

With regard to the Wolffian body, the case is more difficult. Observers appear to agree in placing the appearance of the Wolffian duct within the intermediate cell-mass earlier than that of the tubules, and to indicate the dependence of the latter in some degree on the former. In any case, there appears to be no record of the presence of either meso- or meta-nephros without some duct. Of course, it may be argued that the band posterior to the sex-gland represents the obliterated duct; but there is no evidence in support of such a contention.

ABNORMAL ARRANGEMENT OF THE SPERMATIC
ARTERIES AND OF THE RIGHT CORD AND
TESTES. By T. MARSH, F.R.C.S., &c., *Surgeon to the
Queen's Hospital, and late Demonstrator of Anatomy in
Queen's College, Birmingham.*

A FAIRLY healthy boy, S. M., æt. 3, was admitted into the Queen's Hospital on 19th August 1896, for the radical cure of a large congenital inguinal hernia on the left side. Both testes were in the scrotum, but their relation to the hernial sac was not noted. On 21st August chloroform was administered, and the neck of the sac exposed by the usual incision. When separation of the sac from the constituents of the cord was commenced, an abnormal arrangement was found to exist. Through the external ring, which was large and patulous, two cords were seen to emerge. They were inclosed in one tunica vaginalis, and passed directly downwards and to the right into the scrotum, which was apparently undivided by a septum. What seemed to be a third cord passed from the ring behind the other two almost horizontally towards the right side and extended inwards towards the pubes.

It was not found possible to complete the operation satisfactorily without removal of the testicles, so a ligature was tied high up round the neck of the sac, including the two cords, and the structures below removed, the ring being closed with catgut sutures. Unfortunately, the child died of shock thirty-six hours after the operation. At the autopsy the arrangement of the structures was found to be as follows:—There existed but one vesicula seminalis—that on the left side; it was considerably larger than normal, and in connexion with it there was a very large vas—as thick as an ordinary drawing-pencil—which took the normal course as far as half an inch from the internal ring, where it divided into two of equal size. These pursued their way down the inguinal canal into the scrotum, and were connected with their respective testicles in the usual way. The

right spermatic artery crossed over the middle line about three inches below the umbilicus, and, meeting its fellow of the opposite side just inside the internal ring, joined here with it to form a single trunk, which, passing down the inguinal canal, divided again before reaching the external ring, the two resulting vessels being distributed to the testes in the ordinary manner. The other constituents of the cord were not traced. The third cord mentioned in the description of the operation was composed of fibrous tissue only.

Although the case is interesting from its surgical aspect, it is much more so from a developmental and anatomical point of view. Every departure from the normal is worthy of note, but perhaps especially so is the complete descent of both testes into the scrotum, when associated with other structural deviations. For notes of the case, I am much indebted to my House-Surgeon, Mr R. A. Bennett, M.R.C.S.

CASE OF CLAVICULAR INSERTION OF THE PECTORALIS MINOR. By A. E. TAYLOR, Downing College, Cambridge.

IN the dissection of the right arm of an adult male, there was found a small muscular slip from the upper digitation of the pectoralis minor muscle (coming from the second rib), which passed over the axillary vessels, but under the cephalic vein, and entered the costo-coracoid membrane; here it became tendinous, and was inserted, superficial to the outer part of the subclavius muscle, into the clavicle. It is worth noting that on the same side of the same body there was a well-developed rectus sternalis, whose fibres were not continuous above with the tendon of sterno-mastoid. It passed upwards and inwards from the fifth rib cartilage, to be inserted into the fibrous tissue over the presternum. It is represented on the left side by a tendinous slip, with no muscular fibres. As bearing on the pectoral theory of the origin of this muscle, it may be observed that there was a well-marked deficiency in the portion of the superficial sterno-costal division of the great pectoral which normally arises from the second rib cartilage.

Clavicular insertion of the lesser pectoral is very rare. Wood describes a case in which a slip arising from the first rib was so inserted, and one in which a fascicle which arose from the second rib was attached to the costo-coracoid membrane. He considered these as representing an imperfectly developed sterno-scapular muscle. I am not aware of any other comparable case except that described in a negro by Chudzinski, which was inserted only into a strong arcuate band of the costo-coracoid membrane. The innervation of the slip was not determined, but it being superficial to the subclavius, seems to negative any affinity with the sterno-scapularis. A clavicular insertion of the lesser pectoral in the gibbon is described by Hepburn.

ON THE LINEAR DETERMINATION OF THE HUMAN TOOTH FORM. By W. BOOTH PEARSALL, F.R.C.S.I., Dublin.

FOR some years past I have been engaged in a study of abnormal teeth, of which a fine collection has been made in Dublin. In the best illustrations that I have been able to gather from books I am often at a loss to know what are the points of view from which they have been drawn, as the artist often relies upon mere perspective to show a resemblance to the object which he has depicted. Anyone skilled in close observation can too often see that the artist has not understood the explanatory capabilities of the specimen. This leads to confusion and misunderstanding amongst those who are working at this subject; and, in fact, I have found it impossible to get any two authorities to agree as to the exact characteristics of even the normal human teeth.

Anatomically speaking, the descriptions of the human teeth ought to tally with each other. Amongst the more original, and shall I say skilled, observers, differences in form are described that may be familiar to other observers when described or illustrated from a fixed point of view. Mr Charles Tomes has formed one ideal type of normal human teeth, Mr Andrew Wilson of Edinburgh another, and Mr Humphreys of Birmingham a third. Mr Tomes is alone in showing illustrations of the normal types, which, however, are not all drawn on a definite plan, but in positions which the artist thought would suitably express his idea of the object.

With a view to determining the most characteristic abnormal deviations of the crowns and roots of human teeth, I have endeavoured to borrow from different sources an anatomical and normal set of human teeth, but I have not been successful. It would appear that skilled anatomists and dentists have not yet agreed upon the characteristics that would determine anatomical stability of tooth form. I have spent some time in comparing, classifying, and reducing to order a large number of abnormal teeth. I have not yet succeeded in obtaining a set of normal

teeth, from which starting-point, as it were, to note the departure into what are accepted as abnormal classes.

I have tried the following method as a means by which a number of skilled observers could work on a common basis of accurate investigation. A *diagrammatic* rather than a verbal description would seem to me a more satisfactory way of conducting such an investigation. In order to do this, we can make use of the surfaces of the tooth-crown, which are technically known to dentists all over the world as mesial, buccal, distal, and palatine in the maxilla, and mesial, buccal, distal, and lingual in the mandible. By adopting this method, all observers can treat the tooth-crown and its root or roots as a cube, so that each side of the geometrical form which I have selected would be understood, and the tooth form described with actual precision by making an outline of it. The diagrammatic dental formula of each tooth would therefore run so:—

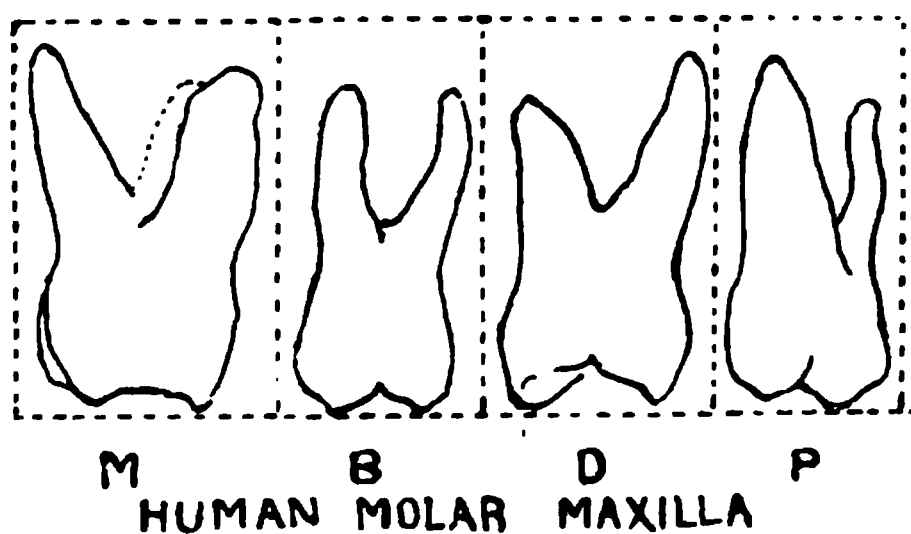


FIG. 1.

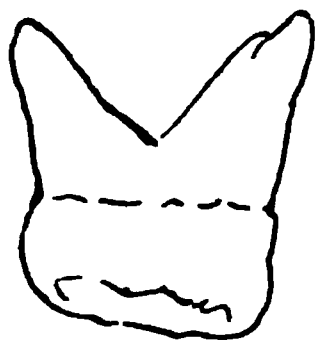
In order to make the investigation useful to dentists, I would figure the neck of the tooth as the upper or lower surface of a tooth in the diagram as well as the crown with its cusps.

By pursuing this line of investigation, I have come across many examples of teeth that have not been described or figured in any book. I have seen some of these types in museums in different places; but, so far, no one appears to have attempted any complete, or shall I say comparatively complete, classification of such interesting parts of our human frame. I shall show my meaning more clearly, perhaps, if I apply this method of observation to the teeth of *Pithecanthropus erectus* brought from Java by Professor Dubois some years ago. Professor Cunning-

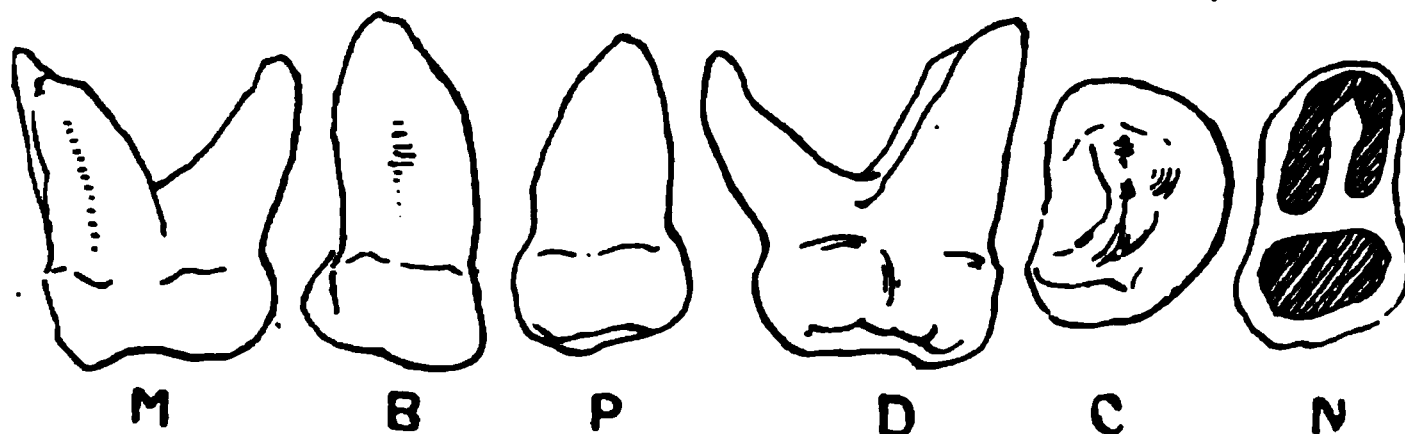
ham brought me, some years ago, the illustration of this tooth in Dr Dubois' memoir, and asked me if I knew of any human tooth that resembled it. It is not an easy question to answer, as, in my opinion, the tooth is inadequately drawn. By the diagrammatic method I have been able to show many points of divergence that are not shown in the illustration as it stands in the memoir.

In the accompanying figure I have drawn the tooth forms

DR DUBOIS'S ILLUSTRATION



RIGHT WISDOM TOOTH MAXILLA



LEFT WISDOM TOOTH MAXILLA

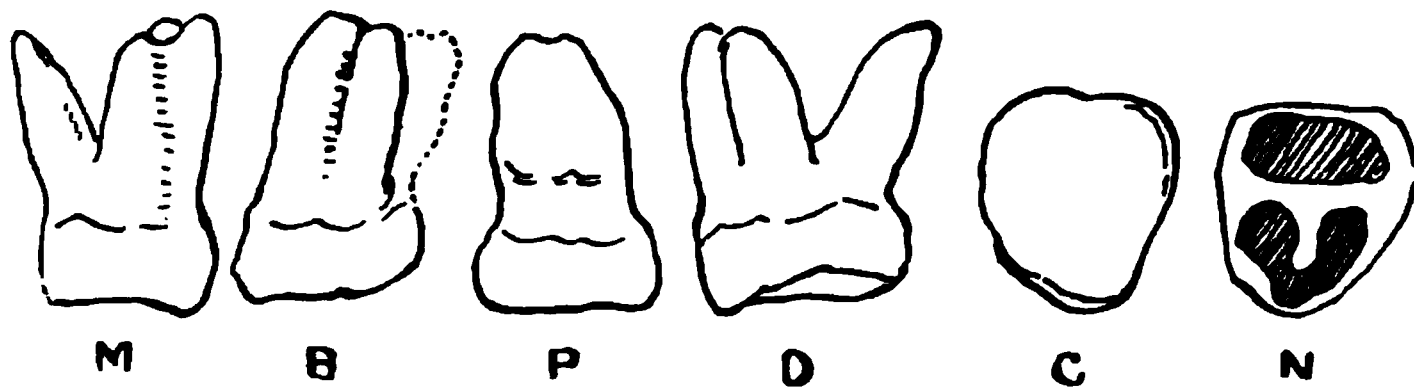


FIG. 2.

simply, so as to show how much more clearly a diagram drawn by a definite method will convey the chief characteristics of any tooth, except, perhaps, the incisors of the pachyderms or rodents, which in some positions would have to be drawn in acute perspective. I have never had the opportunity of examining the teeth of the higher apes by this method. I believe,

however, that it would afford some remarkable figures, and enable us to compare the tooth forms of the primates more easily and directly than we have ever been able to do. Thus, many differences and variations would be ascertained by this systematic method of observation, which it is impossible to convey to observers, who do not see the specimens, by pages of verbal description, however accurate.

THE APERTURA PYRIFORMIS. By Prof. MACALISTER.

MUCH has been written, both by anatomists and by anthropologists, concerning the anterior nasal orifice; but comparatively little attention has been directed to the relations of its bony components to the adjoining soft parts: yet, if we do not take these into account, the study of the skeletal conformation is of little meaning. The key to the understanding of the multiform variations of this aperture is obtained by examining this region in the foetal head.

The margin of the aperture in the foetal head (fig. 1) is divisible into four regions on each side: above, there is the part formed by the lower edge of the nasal bones; secondly, there is the part consti-



FIG. 1.—*a*, Apertura pyriformis of foetal head, front view; *b*, its inferior margin, seen from above.

tuted by the sharp lateral edge of the maxillary border of the opening (fig. 1, *b*); thirdly, there is at the inferior lateral angle of the aperture an intermediate region, internal to which is a fourth part, consisting of a distinct sharp ridge, which, beginning in front at the side of the nasal spine, is directed backwards and outwards until it enters the nasal passage, and is lost posteriorly on the inferior part of the lateral wall of the nose (fig. 1, *b*).

When the soft parts connected with these bony margins are dissected, it is found that the lateral cartilages (fig. 2, *l*) are attached to the edge of the nasal bone and to the trenchant maxillary edge for its upper third. This latter part of the border is occasionally

grooved. To the second third of the border a membrane is attached, and to the lower third the hinder extremity of the detached quadrate cartilages (fig. 2, *s*) are fixed by means of a fibrous lamella, the alar membrane, which on the one side is connected with the perichondrium, and on the other with the periosteum. This membrane extends down below the cartilage, and is continued into the fibro-areolar tissue of the ala nasi.




FIG. 2.—Soft parts attached to the margins of the aperture in the adult. The membranous area *f* extends higher than it does in the foetus; *l.s.l.*, lateral septal ligament; *l.p.*, ligament of the philtrum; *a.l.*, ligament of the inner crus of the alar cartilage (*a*).

To the fourth ridge, which has been called by Allen the *basal marginal line*, but which, from its relations, would be better named the *paraseptal line*, a fibrous tissue is attached, which extends upwards and inwards, and is lost on the lateral surface of the septal cartilage (fig. 2, *l.s.l.*). This forms a lateral ligament for the fixation of this cartilage, and covers the rudimental Jacobsonian cartilage. The third or intermediate area is smooth and scarcely ridged: it extends along the outer side of the paraseptal line, and internal to the termination of the lateral margin. At this region the facial and the nasal areas respectively, without and within the apertura pyriformis, are continuous, not marked off from each other (fig. 1, *b*). On this area there is a mass of fairly tough fibro-areolar tissue, which is connected on the one side with the subcutaneous tissue of the ala nasi, and on the other with the lateral septal ligament. The paraseptal ridge is lost posteriorly on a slightly convex eminence, which descends from the outer wall of the nasal cavity, downwards and inwards to the front of the

anterior palatine foramen: this eminence is hollow, and contains in it the anterior superior dental nerve and its accompanying vessels.

The soft parts in the foetus differ from those in the adult in certain points of arrangement: the attachment of the facial lateral cartilage is closer to the bone than in the specimen from which fig. 2 was drawn; and the lateral membrane *f* in the foetus is shorter, but much wider. In the specimen drawn the cleft between the septal and lateral parts of the cartilage (*c*) at its upper margin was farther out than usual.

The foetal nose is platyrrhine (fig. 3, *a*), its principal characteristics being the wide spread of the inferior lateral angular recess (fig. 3, *b*; *n*) and the wide upper angle. The lower edge of the nasal bones is usually straight or slightly curved, sometimes making the upper margin appear bracket-shaped . In a few skulls the lateral margin is prolonged inwards, and is lost on the middle area, but so close to the septal ridge that the intermediate area is reduced to a minimum: it is, however, seldom quite abolished, so that the presence of a middle area may be regarded as the characteristic mark of the foetal apertura pyriformis.

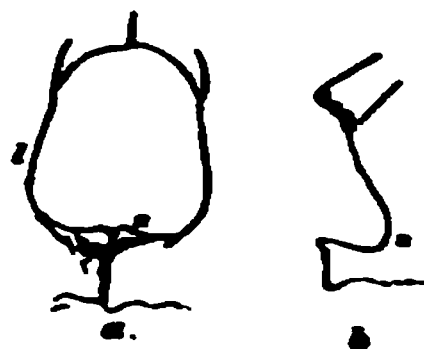


FIG. 3.—Outline of foetal apertura pyriformis. *a*. Front view: *b*, side view.

The varieties of shape met with in the adult crania of different races are chiefly distinguished from each other by the mode of the formation of the lower border, which depends for its shape on the relative positions of the three elevations just described, viz., (1) the lateral margin, (2) the paraseptal line, and (3) the rounded eminence which contains the dental nerve, and which may be called the *anterior dental ridge*. In many South European crania, and in most of those of the yellow races, the lateral marginal edge remains as in the foetus, and does not meet with the outward continuation of the paraseptal line. The persistence of the intermediate area gives to the border a rounded, interrupted appearance, and the relations of the soft parts are practically the same as in the foetus. To this form the name **amblycraspedote** may be given (fig. 7).

In most European crania the intermediate area is abolished, and the post-narial fibrous membrane continuous from the lower

end of the lateral edge to the paraseptal line forms a thinner and more definite layer, into which ossification extends from its bony attachment. The lower border, therefore, appears as a trenchant rising edge, formed of the confluent lateral margin and paraseptal line, which masks the anterior dental ridge (fig. 4). To this form the name **oxycraspedote** may be given.

In these crania the teeth are smaller and the whole alveolar arch is shorter; so the incisor alveoli do not extend forwards to the same proportional distance as they do in the crania of the other groups. The nasal septum, however, does not commensur-

FIG. 4.—*Oxycraspedote* form of *apertura pyriformis*.

ately diminish; therefore the nasal spine, which remains to support the lower and front part of its cartilaginous portion, projects prominently in front of the plane of the incisor alveoli. The paraseptal line is, in consequence, for the most part also in front of the level of the lower end of the lateral margin. In consequence of the narrowing of the *apertura pyriformis*, due to the diminished size of the maxilla, these two lines come in contact at the point when the paraseptal line enters the nasal cavity, and at the period of the second dentition usually become confluent.

In the skulls of the mesodont and the mesognathous races the anterior dental ridge is larger, and by its prominence it obscures the paraseptal line externally, giving to the lower lateral margin

of the aperture a blunt rounded appearance, while the lower end of the lateral margin of the opening is continued forwards and inwards on a lower level on the maxilla, above the incisor alveoli. Between this line and the prominent anterior dental ridge there is an oblique prenasal fossa, scaphoid in shape, covered in the recent state with a fibrous sub-mucous tissue, which is continuous internally into the ligament of the septal cartilage, while externally it underlies the *limen vestibuli* or marginal mucous fold, which bounds the vestibulum nasi posteriorly, and is con-

FIG. 5 — Exaggerated example of the bothrocraspedote form of aperture, from the skull of a Kanaka from Oahu. *p.n.f.*, prenasal fossa; *p.s.*, paraseptal line; *d.*, anterior dental ridge. This form seems to be common among Polynesians.

tinuous with the alar membrane. This form of aperture may be called **bothrocraspedote**. This is an exaggeration of the fetal condition, modified by the inward extension of the lateral margin above the incisor alveoli, on a level below the nasal spine.

In the extreme modification of the lower lip of the opening met with in macrodont and prognathous skulls, notably in many Australians, the lower edge of the lateral lip is continued downwards, to be lost on the front of the lateral incisor alveoli. In

consequence of the obliteration of the inward continuation of this line, the floor of the nose is continued forwards without any line of demarcation from the anterior dental ridge into the facial surface of the alveolar process; and the lipless lower edge of the pyriform aperture appears as in anthropoids like a gutter, margined on each side by the prominent canine alveoli. This form may be called **orygmocraspedote** (fig. 6). Intermediate varieties between these type-forms are not uncommon.

In pyriform apertures of all kinds the lateral maxillary edge is thin and usually sinuous, with a slight forward convexity

FIG. 6.—Orygmocraspedote aperture in the skull of a S. Australian. The condition is accentuated on the left side on account of the loss of the left median incisor, which has been removed in the initiation ceremony at puberty.

below the naso-maxillary suture. The most prominent part of this swelling corresponds to the lower angle of the attachment of the lateral expansion of the septal cartilage. The angle made by this edge with the line of the naso-maxillary suture usually increases with the increase of proportional length of the nose, and diminishes with increase of width.

The upper edge of the aperture is usually damaged in museum specimens. When perfect, the outline varies considerably, the two extremes being (1) that in which there is an acute median point formed by the downward prolongation of the inner angle of the contiguous nasal bones; external to this there is a deep notch on each side, outside which the margin slopes more or less irregularly downwards and outwards to the external angle at the

lower end of the naso-maxillary suture. This condition is the commonest in the white races (as in fig. 4).

(2) The second extreme is that in which angles and notch have disappeared, and the lower border is a straight or slightly concave transverse line. This, which is the foetal condition, is found in many of the black races (figs. 5 and 6). These varieties have been carefully described by Manouvrier.

The shape of the aperture in the foetal and infantile skull is somewhat quadrate, with a wide flat lower and an arched upper boundary (fig. 3). This variety, the *forma infantilis* of Mingazzini, persists in many of the black races. In the European it is usually shaped like an elongated pear with a double stalk (fig. 4), the rising, nasal spine giving to the lower edge a notched appearance which has been compared to the shape of a heart on a playing card (*forma anthropina*). To the variety with a pre-nasal fossa (fig. 5), the name *forma prenasalis* is given; and to the variety with the simian alveolar gutter that of *forma naso-alveolaris* (fig. 6). These subdivisions generally agree with those described by Broca and Topinard, but the names I have suggested above have the advantage over those suggested by Mingazzini in being more definite.

The following variations are shown by the nasal spine. This process is the median forward projection of the front end of the crista incisiva, which receives in its hollowed upper surface the anterior inferior border of the septal cartilage. It is a constant element in the human face, and is absent in anthropoids owing to the great size of the incisor alveoli, whose forward projection on each side causes the groove for the front end of the septal cartilage to appear as a fossa rather than as a spine. The spine is thus masked rather than abolished.

In most male European skulls the spine is a sharp spur projecting horizontally forwards (fig. 4). From its under surface a median ridge, the median maxillary crest, descends along the suture towards the alveolar point. To this is attached a ligament for the philtrum (fig. 2, *l.p.*), whose upper border is attached to the inner crura of the alar cartilages (fig. 2, *a.l.*). This oxyacanthic condition is usually present in the infants of the white races at birth.

In the crania of the yellow races the spine is an angle at the

junction of the crista incisiva and the median maxillary crest, but projects little beyond these. This condition may be called **lophacanthic** (fig. 7). In the black races the median crest is feebly marked, and the nasal spine is partly masked by the large incisive alveoli. This **cryptacanthic** condition is present in the skulls of some Australians, Tasmanians, and Bushmen (fig. 6).



FIG. 7.—Amblycraspedote form of the aperture in the skull of a Carib.
The nasal spine is lophacanthic.

From the comparison of the margins of this aperture in skulls showing these different conditions, it becomes manifest that the oxyacanthic and oxycraspedote aperture depends on microdontism and orthognathism; while, for the most part, the cryptacanthic and orygmocraspedote form is correlated with the opposite conditions of macrodontism and prognathism. The nasal cartilages of the Australian are little, if any, larger than those of the European.

Note.—I have not referred in the text to the interesting paper by Prof. Havelock Charles on this subject (*Journal of the Asiatic Society of Bengal*, lxiii. Part III. No. 1, 1894), as the author does not therein refer to the causation of the varieties which he describes. His classification into cordiform and rotund forms—the former being sub-divided into regular, lyrate, and irregular—does not cover the whole range of forms met with in the survey of the aperture in all the races of man.

FURTHER OBSERVATIONS UPON THE FORNIX, WITH
SPECIAL REFERENCE TO THE BRAIN OF *NYCTO-
PHILUS*. By G. ELLIOT SMITH, M.D. (Sydney), St John's
College, Cambridge.

THERE are certain features in the arrangement of the fibres of the fornix during their course in the cerebral hemisphere which it was impossible to discuss adequately in my contribution to the last number of this *Journal*¹ without unduly increasing the size of that communication. In the consideration of the peculiarly simple arrangement of the cerebral commissures and fornix in a small Australian bat, *Nyctophilus Timoriensis*, with which the present communication is mainly concerned, it will be convenient to discuss some of the wider questions of the morphology of the fornix to which a mere passing reference was made in the work quoted. The reasons for the peculiar suitability of the brain of *Nyctophilus* for this purpose have already been partly explained,² and will, moreover, become apparent from the present account.

The figure which illustrates this description represents a sagittal section through the forebrain of *Nyctophilus*, passing quite close to the mesial plane. This figure is diagrammatic inasmuch as certain obliquely running fibres, only a short part of whose course would be found in a single sagittal section, are represented lying in the plane of this section. This has been done to obviate the necessity of a series of sections differing merely in detail.

For the material used in this investigation I am indebted to the generosity of my friend Dr Robert Broom.

The anterior pole of the hemisphere is formed by the olfactory

¹ "The Relation of the Fornix to the Margin of the Cerebral Cortex," this *Journal*, vol. xxxii. part 1, October 1897.

² "The Origin of the Corpus Callosum : a comparative study of the hippocampal region of the cerebrum of Marsupialia and certain Cheiroptera," *Transactions of the Linnean Society of London*, vol. vii. part 3, June 1897.

bulb, which is capped, as usual, with a layer of glomeruli (*Gl*) and olfactory nerve fibres (*F.o*). The bulb is joined to the rest of the hemisphere by means of its peduncle, whose mesial wall (*P.o*) is in direct continuity with that of the cerebral hemisphere.

The mesial wall of the hemisphere is divided into two sharply differentiated areas by means of a line (*H''*) which extends from the olfactory peduncle in front, backward and slightly upward to the tip of the corpus callosum (*a*).

In the *Transactions of the Linnean Society*,¹ it was shown that the hippocampus which fringes the margin of the cerebral hemisphere posteriorly reaches as far forward as the splenium of the corpus callosum, to become continuous with a band of grey substance which covers the upper surface of the diminutive dorsal commissure (*loc. cit.*, plate xvi. fig. 17, *hip*). It was then shown that this grey supra-commissural band was the vestige of part of a more extensive hippocampal arc, but that, whereas in the most caudal part of its supra-commissural course it still maintained the distinctive features (*vide* this *Journal*, *loc. cit.*, fig. 19, page 46) of a hippocampus, it became reduced anteriorly to an extremely insignificant group of cells (compare *Trans. Lin. Soc.*, *loc. cit.*, plate xvi. fig. 16), which were only with difficulty recognisable as hippocampal remains. These hippocampal remains are not confined to the supra-callosal region of the hemisphere, but extend forward (along the line *H''*) as far as the *pedunculus olfactorius*. In this pre-commissural part of its course the hippocampal vestige consists of a fairly well defined column of small cells lying very close to the surface along the ventral margin of the true cortex. In other words, the typical cortex or pallium (*Pa*) is placed upon the dorsal side of the hippocampal vestige (*H''*). And as the section represented in the figure is very close to the mesial plane, the superficial layer of the cortex, which is free from any collection of nerve fibres, comes into the plane of the section. But in the superficial layer of the infra-hippocampal region of the mesial wall, which is formed mainly of *pre-commissural body* (*P P'*), we find a very abundant arrangement of nerve fibres belonging to the fornix system. The two cerebral hemispheres are bound together as usual by the lamina terminalis,

¹ *Loc. cit.*

containing two sets of commissural fibres, a dorsal and a ventral.

The dorsal commissure (*C W*) presents a peculiar inverted V-shaped appearance when viewed in sagittal section in *Nyctophilus*. The posterior limb (*W*) is approximately vertical, and at its upper and thicker extremity (splenium) meets the anterior limb (*C*), which slopes forward and slightly downward, and at the same time tapers to a pointed anterior extremity. The two limbs of this commissure are widely separated, the postero-superior part of the *pre-commissural body* (*P*) filling up the interval between them. The whole of the vertical posterior limb (*W*), as well as the greater part of the splenium, is composed of fibres, which are brought in the fornix from the hippocampus of one or the other hemisphere, to cross in this situation to the fornix of the opposite hemisphere. It is therefore the hippocampal or fornix commissure—the *psalterium* of human anatomy. The majority of the fibres of the anterior limb of the dorsal commissure (*C*) are derived from the general cortex (*Pa*), and constitute, therefore, the corpus callosum proper.

In the contribution to the last number of this *Journal* (*loc. cit.*) it was pointed out that when the corpus callosum (*C*) increases in size and elongates, the main mass of the hippocampal commissure maintains its original position unchanged. At the same time, a series of commissural fibres of the fornix become spread out between the upper extremity of the main mass of the hippocampal commissure and the splenium or posterior extremity of the corpus callosum. In the case of animals like the rabbit (Koelliker) and hedgehog (this *Journal*, p. 45), in which a definite 'infra-splenic hippocampal flexure' exists, these two regions of the hippocampal commissure may always be distinguished. In the case of such animals it has been customary, since the work of Gudden and Ganser, to call the main mass of the hippocampal commissure (this *Journal*, p. 41, fig. 10; p. 45, fig. 17, *W*) the *psalterium ventrale*, and the upper extended and attenuated part of the same commissure (*W'*) the *psalterium dorsale*. The qualifying terms 'dorsale' and 'ventrale' refer to the region of the alveus coating the tip of the hippocampal flexure, from which the commissures appear to spring (*vide* p. 44, fig. 15, *h* and *w*: the *psalterium dorsale* is not labelled,

EXPLANATION OF REFERENCES
IN FIGURE.

- C, *Corpus callosum*.
C.e.g, Commissure of the corpora quadrigemina.
C.f, *Columna fornix*.
C.h, *Commissura habenularum*.
C.p, *Commissura posterior*.
D, *Dentata*.
D.f, *Decussatio fornicis*.
F.l.p, *Fasciculus longitudinalis posterior*.
F.m, *Fasciculus medialis*.
F.o, *Fasciculus opticus*.
F.l.m, *Fasciculus thalamo-mammillaris*.
F.teg.m, *Fasciculus tegmento-mammillaris*.
G.h, *Glomerulus habenulae*.
Gl, *Glomeruli*.
H, The situation of the pre-commissural vestige of the hippocampus.
L, *Strius Lancisi* contained in the *Induratum griseum*.
M, *Nucleus medialis corporis mammillaris*.
Op, *Chiasma opticum*.
P, *Corpus pre-commissurale*.
P', *Part anterior corporis pre-commissuralis* (*septum pellucidum*).
Pa, *Pallium illaria*.
P.c.m, *Pars commissa*.
P.in, *Pars interna*.
P.l.a, *Pars lateralis*.
P.t.p, *Pars transversa*.
P.o, *Pars optica*.
R, *Rostellum*.
S.m.f, *Sulcus medianus fornicis*.
Str.gr, *Stratum griseum*.
offacturi, *officium acturi*.
V, *Commissura anterior*.
W, *Commissura hippocampi*.



SAGITTAL SECTION OF THE FOREBRAIN OF *Nyctophidius Tlaxienseis*—(Weigert stain).

but is immediately below *C*), rather than to the absolute positions of the commissure when seen in profile.

In *Nyctophilus* the corpus callosum (*C*) is such an insignificant structure that it has produced little or no effect upon the hippocampal commissure (*W*). Hence there is no distinction between its upper (*psalterium dorsale*) and lower fibres (*psalterium ventrale*).

The ventral or inferior commissure (*V*) appears to consist (in specimens treated with some medullary stain) of two distinctly separated bundles of fibres. The *pars olfactoria* appears to lie some distance below and slightly in front of the rest of the commissure. But this separation is more apparent than real, for the interval seems to contain a number of fibres which are unaffected by the medullary stain.

In passing, we may note the relationship of the roof of the forebrain (*tela choroidea*, *R*) to the dorsal commissure. This is of considerable interest to the comparative anatomist who concerns himself with the reptilian and amphibian brain, but the importance of which has been greatly exaggerated by a certain class of writers. In monotremes, as well as in most sub-mammalian brains, the epithelial roof of the forebrain extends forward *above* the dorsal commissure, to be attached to the anterior corner of the thickened upper extremity of the lamina terminalis, which serves as a matrix for the dorsal commissure. In this way a small recess of the median ventricular cavity is produced upon the dorsal aspect of the dorsal commissure. Many writers have seized upon this simple fact, and spoken of the dorsal commissure as 'infra-ventricular,' as a 'commissure of the floor,' in contradistinction to the 'corpus callosum,' which they speak of as 'supra-ventricular,' or a 'commissure of the roof.' In doing so they grossly exaggerate the importance of a very simple fact, and base their argument upon a most fallacious footing. The choroid plexus of the lateral ventricle in *Nyctophilus* establishes a peripheral attachment to the ridge formed by the fimbria in the whole extent of the latter structure. When the fimbria reaches the lamina terminalis anteriorly, the epithelial choroidal fold of each hemisphere becomes mesially continuous with the *tela choroidea*, which ends anteriorly by joining the dorsal extremity of the

lamina terminalis. The situation of the dorsal extremity of the lamina terminalis is indicated (*vide* figure) by a small nodule of grey matter placed upon the caudal aspect of the hippocampal commissure. (See also this *Journal*, *loc. cit.*, figs. 10 and 23, in which *R* is the *tela choroidea*, and *W* the hippocampal commissure.) This nodule appears to be identical with the structure of which Burt Wilder speaks somewhat vaguely as the '*crista fornicis*' ("Neural terms," *Journal of Comparative Neurology*, vol. vi., and elsewhere). In most mammals the raising of the corpus callosum and the upper part of the hippocampal commissure in the course of development (this *Journal*, *loc. cit.*, p. 41) raises part of the lamina terminalis (*i.e.*, the matrix of these commissures) far above the level of the original upper extremity of the terminal lamina. But the situation of this original upper extremity is indicated in such cases by the place of attachment of the membranous roof to the matrix of the main mass of the hippocampal commissure (*vide* figure).

THE FORNIX IN *Nyctophilus*.

The vast majority of the fibres of the *columna fornicis*—the post-commissural fasciculus of the *fornix longus* of Forel—are brought up to the *pre-commissural body* or *septum pellucidum* (*P*) as one of the series of constituents of the fimbria. And in a sagittal section they may be seen entering the *corpus præ-commissurale* immediately in front of the hippocampal commissure (*W*), whose fibres are likewise conducted forward from the hippocampus in the fimbria. The fibres of the former arch downward and then backward in the septum, converging to form a compact strand, which extends behind the anterior commissure (*V*) to enter the optic thalamus (*c.f.*). This group of fibres of the *columna fornicis*, which make their appearance in the septum immediately in front of the *psalterium* (*W*), is not disturbed in any way by the development of the corpus callosum, and maintains an exactly similar course in brains such as those of monotremata and marsupialia which lack a true corpus callosum, and in other mammalian brains in which this commissural band is highly developed (compare figs. 6, 7, and 23 this *Journal*, *loc. cit.*, vol. xxxii.; also fig. 3 this *Journal*,¹ vol. xxxi.).

¹ "The Fornix Superior."

But a not inconsiderable number of fibres of the *columna fornicis* come from the *striae Lancisii* (*L*). These fibres reach the *pre-commissural body* either by perforating the corpus callosum (*C*) or by passing around its anterior extremity, and then extend downward and backward to associate themselves with their serial homologues above the anterior commissure. It is obvious that this group of fibres will be considerably affected by the development and increase in size of the corpus callosum, whose fibres, like so many strings between the two hemispheres, will deflect from their course the longitudinally running fibres of the fornix as the corpus callosum becomes raised and longitudinally extended. Moreover, the atrophy of the dorsal part of the hippocampal arc consequent upon the development of the corpus callosum further affects this group of fibres by reducing their number.

In this way the fibres of the *columna fornicis* separate themselves into two natural groups, a ventral and a dorsal. The *ventral group*, whose volume and course are undisturbed by the transformation of the great dorsal commissure, includes in most mammals the great majority of the fibres of the fornix-column, because the dorsal group becomes so extensively reduced. The *dorsal group* is distinguished by the fact that the course of its fibres becomes deflected by the corpus callosum, and that they are comparatively few in number.

In *Nyctophilus* the course of the fibres of the dorsal group is affected only to a very slight degree, because the corpus callosum is so rudimentary, but there is a marked diminution in the number of its fibres, because the dorsal limb of the hippocampus is degenerate.¹

The *fasciculus præ-commissuralis*, or 'pre-commissural fibres' of Huxley, demands no further description, since it exactly conforms to the description given in the last number of this *Journal*. Like the *columna fornicis*, it may be divided into a ventral group of fibres which make their appearance in the septum immediately in front of the main mass of the hippocampal commissure (*W*), and a less abundant dorsal group of fibres which come from the

¹ In this *Journal*, vol. xxxi., *loc. cit.*, the erroneous statement was made that the dorsal limb of the hippocampus was *not* degenerate,—p. 85.

striae Lancisii, passing either in front of (a) or through the corpus callosum.

In sagittal sections which pass close to the mesial plane in the brain of *Nyctophilus*, a very distinct and compact strand of nerve fibres (*L*) may be noticed pursuing an antero-posterior course (*i.e.*, in the plane of the section) on the upper surface of the corpus callosum. These are the fibres of the *striae Lancisii*, and constitute the *fimbria* or *fornix* of the *supra-commissural hippocampal vestige*. The hippocampal vestiges lying upon the dorsal surface of the corpus callosum are joined to one another by a mesial film of grey matter—*indusium verum* (this *Journal*, fig. 19, p. 46, *i*), the whole lamina of grey matter constituting the *indusium*, as that term is generally understood.

It will obviate a considerable amount of confusion if the term '*striae Lancisii*' be restricted to the nerve fibres which are situated in the *indusium*, rather than to the complex of fibres and grey matter, as is so often done. In this sense, it may also be used to include not only the mesial *striae strictu*, but also the lateral *striae* (*tæniæ tectæ*). In other words, the term '*striae Lancisii*' may most conveniently be interpreted as the whole system of fibres (*i.e.*, the fornix) of the vestigial hippocampus.

In the brain of *Nyctophilus* it is possible, so diminutive is its size, to trace readily the constituent fibres of the *striae Lancisii* throughout not only the whole length of their supra-callosal course, but even further.

Thus, if the fasciculus be traced forward, its constituent fibres will be found to diverge widely as they descend (a) in front of the corpus callosum. A considerable number of fibres of this diverging brush may readily be followed in their vertical course to associate themselves with the other fibres of the *fasciculus præ-commissuralis* (b). Others, again, may be as readily followed in the whole of their oblique course backward and downward to enter into the constitution of the *columna fornicis* (c.f). A continuous film of fibres which occupy what we may call the 'septal region' (*P'*) stream from the *striae Lancisii* downward through the corpus callosum, to reach the same destinations as those which surround the anterior pole of the corpus callosum. But these are not the only constituents of the *striae Lancisii*.

For if we examine the brush of nerve filaments which lie in

front of the corpus callosum (*a*), it will be found that in addition to the two sets of fibres which have just been mentioned, there is a group of very delicate medullated nerve fibres, which extend forward in (or at the lower margin of) the pre-commissural vestige of the hippocampal arc (*H''*). These delicate fibres may be traced as far forward as the olfactory peduncle, but it is not possible to state definitely their anterior attachments. They undoubtedly correspond to the well-developed bundle of fibres to which I have directed attention in the brain of monotremes and marsupials as the *fasciculus marginalis*. Other fibres of a similar character proceed backward below the corpus callosum. In the *striae Lancisii* these three sets of fibres—*fasciculus marginalis*, *fasciculus præ-commissuralis*, and *columna fornicis*—are collected into a compact strand (*L*). If this strand be traced backward many of its fibres will be found to extend into the *stratum moleculare* of the fascia dentata (*D*), apparently to end there. Others extend into the alveus of the hippocampus, which is in direct continuity with the deeper or fibre layer of the *indusium*.

Arguing from our knowledge of the arrangement of the three series of constituent elements in *Ornithorhynchus* (this *Journal*), it seems justifiable to infer that the fibres of the *striae Lancisii* which proceed backward into the superficial layer of the fascia dentata belong to the *fasciculus marginalis*, whereas those fibres which may be traced into the alveus of the post-commissural hippocampus belong to the *fasciculus præ-commissuralis* and *columna fornicis*.

In all the brains which I have examined, including those of the hedgehog, cat, and man, fine medullated nerve fibres may be traced from the posterior extremity of the *striae Lancisii*, more especially from the mesial *striae*, into the molecular layer of the tapering dorsal extremity of the fascia dentata. In these same animals it is possible to trace fibres from the anterior extremity of the *striae Lancisii* around the *genu corporis callosi* through the *gyrus subcallosus* (*pre-commissural body*) to the neighbourhood of the olfactory peduncle.

In the last number of this *Journal* we saw the *fasciculus marginalis* pursuing its oblique course upward and backward immediately at the ventral margin of the fascia dentata (*loc. cit.*,

figs. 5 and 6, 5). In the cerebral hemisphere of most mammals a small longitudinal tract of fibres may be recognised at the margin of the fascia dentata, and forming a constituent of the fimbria, or, more commonly, the extra-ventricular alveus.

With the knowledge that in *Ornithorhynchus* an unbroken series of fibres may be traced from the mesial surface of the olfactory peduncle into the molecular layer of the fascia dentata, and that the corpus callosum makes its appearance upon the ventral side of this *marginal bundle*, it seems justifiable to infer, from the scattered data which have just been enumerated, that a *fasciculus marginalis* is present in the brains of *Nyctophilus*, *Erinaceus*, *Felis*, and *Homo*.

It is in the highest degree probable that this series of fibres constitutes one of the paths by which olfactory impulses may reach the fascia dentata and hippocampus. Yet it seems probable that there must be other and much more abundant fibre-systems in this same pre-commissural region, serving as a bond between the olfactory apparatus and the hippocampus.

For many years anatomists have been convinced that some intimate connection exists between the olfactory bulb and the hippocampal formation, but we are still in the dark regarding the exact nature of the anatomical bond. The much quoted observations of Zuckerkandl cannot be regarded as a final solution of this problem. But there are many facts which the comparative study of this subject brings to light, which, if they do not supply the necessary direct evidence, are highly suggestive of the probable solution of the problem.

We have already seen that in the *Monotremata* a highly developed hippocampal formation is found in the situation which corresponds to that occupied by the supra-commissural (*L*) and pre-commissural vestiges (*H''*) in *Nyctophilus*. In reptiles, the homologue of these parts of the hippocampus forms the whole of the mesial wall (corresponding to the situation of the pallium (*Pa*) in *Nyctophilus*) which lies above the pre-commissural body, and even extends on to the dorsal aspect of the brain. As the hemisphere of reptiles has only a very slight caudal extension, it follows that the great bulk of the hippocampus lies either above or in front of the commissures. In the amphibia the rudimentary hippocampus occupies even a more

completely forward position. We have therefore some justification for concluding that the primitive and essential position of the hippocampus is in the mesial wall of the hemisphere, in direct continuity with the mesial wall of the olfactory peduncle and bulb. In view of this fact, it is in the highest degree probable that the anatomical link between hippocampus and olfactory bulb will be found in the fibres of the *pre-commissural body*.

If we examine the supra-commissural structures in a coronal section, we shall find that the *striae Lancisii* have no definite lateral border. The transverse sections of its fibres are in unbroken series with longitudinal fibres which are placed in the medullary matter of the adjacent general cortex, and which it is customary to distinguish as the *cingulum*. The exact relationship between these two series of fibres has been represented schematically in another place.¹ The distinction between the two series of fibres is that the *cingulum* is a derivative of the pallium, whereas the *striae Lancisii* belong to the hippocampal vestige. But at the lateral border of the *indusium*, where the two series of fibres intermingle, it is not easy to decide to which group any given fibre belongs. Koelliker, in all his recent observations upon the *fornix superior*, attributes a pallial origin (*i.e.*, from the gyrus fornicatus) to some of its fibres. I have carefully examined numerous sections of various brains in search of definite evidence upon this point, because, as I have pointed out on several occasions, comparative data do not favour the idea of a pallial origin; but in no case have I been able to trace any fibres of the *fornix superior* into any other supra-callosal region than that of the *indusium griseum*, which we know to be a purely hippocampal formation.

The important contributions to the literature of the fornix which have emanated from von Koelliker during the last three years have cleared the way for further investigations upon the subject. As a critical review of past work, and as a minute and exhaustive study of the nature of the fornix in the rabbit, cat, and man, these classical memoirs must form the foundation upon which all further additions to our knowledge of this subject will be built up.

¹ "The Morphology of the Indusium and Striae Lancisii," *Anat. Anz.*, xiii. B 1., Nos. 1 and 2.

In this discussion I propose to examine briefly, in the light of comparative data, the conclusions at which Koelliker arrived from the study of these three highly specialised types.

According to Koelliker (*Handbuch der Gewebelehre des Menschen*, Bd. ii., Zweiter Hälfte, 1896, p. 774), the fornix consists of a fibre-mass, which appears to be the continuation of the *fimbria* or *limbus cornu Ammonis*. He further describes this complex of fibres as consisting of two parts—the *fornix longus* of Forel (to which he gives the alternative name *fornix superior*), and the rest of the fornix, which he distinguishes as the *fornix inferior*. He further points out that the latter corresponds to the whole of what has hitherto been called 'fornix' simply, and is nothing else than the *fimbria* or *limbus cornu Ammonis*. If this nomenclature be adopted, the terms *fornix superior* and *fornix inferior* will be applied to what are in the main merely different parts—"septal" and "post-septal" respectively—of one and the same fibre-mass. The object of such a nomenclature is not very apparent. Especially is this the case in regard to the term '*fornix inferior*,' seeing that, as its author has pointed out, we already have two synonymous terms in '*fimbria*' and '*limbus*.'

Some time ago I ventured to suggest a more exact definition and a more limited application of the term '*fornix superior*' than its author had suggested ('*fornix superior*,' this *Journal*, vol. xxxi., October 1896). As Koelliker applied this term, i.e., as synonymous with his interpretation of the *fornix longus*, it was difficult to understand his limitations of it ('*Ueber den fornix longus, etc., etc.*' Vierteljahrsschrift der Naturforschenden Gesellschaft in Zurich, xli., 1896, Jubelband). For while he uses the term in many places as a synonym for the septal part of the *columna fornicis*, yet at other times he speaks of it as including all the *fibræ perforantes*. Now, many of these fibres are constituents of the pre-commissural bundle, which he excludes from his *fornix superior*.

In 1896 (*loc. cit.*) I suggested the use of the *fornix longus* in what seemed to be the original sense of Forel, i.e., as all the longitudinal uncrossed fibres of the fornix system. The term *fornix superior* was applied in the same communication to all those fibres of the *fornix longus*, which do not enter the septum along with those commissural fibres which form the main mass of the *psalterium*.

This definition corresponds to what I have in the present communication (*supra*) spoken of as the dorsal group of fibres of the *columna fornicis* and *fasciculus præ-commissuralis*. In order not further to prejudice Koelliker's term '*fornix superior*,' I propose to use the designation '*fornix dorsalis*' for all those uncrossed fibres of the fornix whose arrangement is disturbed by the development of a corpus callosum, and which arise from or end in the dorsal limb of the hippocampal arc.

The *fornix dorsalis* thus includes the *striae Lancisii* and all the fibres connected with these *striae*, as well as the uncrossed fibres which arise from the subsplenial hippocampal flexure.

The term '*fornix ventralis*' might then be appropriately applied to all the other uncrossed fibres of the fornix, *i.e.*, those undisturbed by the developing corpus callosum.

The term '*fornix obliquus*,' which Honegger and Koelliker apply to certain fibres of the pre-commissural bundle which spring from the hippocampal flexure, is of doubtful significance and no obvious value, and might well be discarded.

The fornix, then, might be divided up in this manner:—

Fornix	{	<i>fornix transversus</i> (<i>psalterium</i>).
		<i>fornix longus</i> { <i>fornix ventralis</i> . <i>fornix dorsalis</i> . ¹
	{	<i>fornix ventralis</i> { <i>fasciculus post-commissuralis</i> (<i>columna fornicis</i>). <i>fasciculus præ-commissuralis</i> .
		<i>fornix dorsalis</i> { <i>fasciculus post-commissuralis</i> . <i>fasciculus præ-commissuralis</i> . <i>fasciculus marginalis</i> .

The belief in an origin of the *fornix longus* from the gyrus fornicatus has led to a peculiar, and I believe fallacious, train of argument concerning the morphology of the mesial wall of the hemisphere in mammals, which has resulted in a complete misconception of the fundamental disposition of the cerebral cortex in all other vertebrates.

In 1894 Koelliker first gave his support to the view that the *fornix longus* had an origin from the gyrus fornicatus ('*Ueber den Fornix longus von Forel*,' etc., Verhandl. d. anatom.

¹ In this system of nomenclature the *fornix ventralis* represents the group of uncrossed fibres corresponding to the *psalterium ventrale*, while the *psalterium dorsale* would include the crossing fibres corresponding to the *fornix dorsalis*.

Gesellsch. in Strassburg, May 1894). In reviewing this work shortly afterward, Edinger uses the term '*Randwindung*' to express the idea of the gyrus fornicatus, in spite of the fact that this term as well as the name '*gyrus limbicus*,' which he subsequently uses as a synonym, have both been used in quite a different sense (Edinger, '*Leistungen auf dem Gebiete der Anatomie de Centralnervensystems*,' Schmidt's Jahrbücher, Bd ccxvi.). For both of these terms have been applied to the *indusium griseum* (Schäfer, *Quain's Anatomy*, vol. iii. part i, 1893, p. 159).

In 1896 Edinger speaks of the *gyrus limbicus* in mammals as the frontal continuation of the 'Ammonsrinde,' i.e., hippocampus, "welche nicht mehr engerollt ist und über dem Ventrikel liegt." He further adds, "Ich halte es für wahrscheinlich, dass in dem Rindengebiete, welches bei den Reptilien als Ammonsrinde bezeichnete wurde, die Elemente des Gyrus limbicus und der Ammonsrinde gegeben sind" (*Unters. üb. d. vergl. Anat. d. Gehirns* iii. Senckenberg. Abhandl. 1896).

Thus, while Edinger undoubtedly uses the terms '*Randwindung*' and '*gyrus limbicus*' in the unusual sense as synonyms for the anterior part of the *gyrus fornicatus*, yet at the same time he speaks of this structure as the forward continuation of the hippocampus, as though the latter were identical with the pallial area generally but confusedly known as the 'hippocampal gyrus.' The first quotation is so vaguely expressed that one might easily believe the author to be using the term '*Randwindung*' in its more usual sense as the *indusium* (Zuckerkandl's *gyrus supra-callosus*), in which case the statement would be quite intelligible. But this interpretation the author never intended, for in his *Vorlesungen* (1896) he speaks of the *indusium* (*striae longitudinales Lancisii*) as the forward continuation of what he somewhat rashly speaks of as the "schon im Ammonshorne atrophischen Windung, des Gyrus dentatus."

We begin to gain some idea of the meaning of these extraordinary statements when the writer, in speaking of the *fornix longus*, defines it (*Vorlesungen*, p. 210) as those fibres "welcher aus demjenigen Theile der Randwindung, welcher nicht zum Ammonshorne sich einrollte, aus dem Gyrus limbicus." The idea expressed in this statement seems to be the harmonising

of the morphology of the cortex with the supposed grouping of the fibres derived from it. In other words, because the fornix springs posteriorly from the hippocampus, and anteriorly from the gyrus fornicatus (as Koelliker and Edinger believe), Edinger argues that the gyrus fornicatus is the anterior extension of the hippocampus. Thus (on page 168) he says again that in higher mammals, in consequence of the development of the corpus callosum, the fornix fibres from the Ammonshorn are separated from those which arise from the more anteriorly placed part of the *Randwindung* (meaning the gyrus fornicatus).

By introducing this idea of a *Randwindung*, which groups gyrus fornicatus with hippocampus, Edinger attempts a morphological justification for Koelliker's supposed origin of the fornix from the former structure. In his *Gewebelehre*, the latter distinguished histologist quotes with approval Edinger's interpretation, and makes a clear statement of his view, which is quite free from any ambiguity. He thus distinctly, but unintentionally, reduces the argument to a *reductio ad absurdum*.

Thus, on page 825, in speaking of the reptilian brain, he says, "Edinger hat schon eine Andeutung, ob dieser Fornix der Reptilien nicht dem *Fornix longus* der Säuger entspreche, die ich voll unterstützen möchte. Die mediale Wand des Vorderhirnes der Reptilien entspricht ja nicht nur Ammons-falte, sondern auch dem *Gyrus fornicatus* der Säuger, aus welchem der *Fornix longus* entspringt. Ein *Fornix inferior* kann bei der Reptilien kaum vorhanden sein, da auch das Ammonshorn, in welchem derselbe entspringt, nicht gebildet ist."

Edinger and Koelliker regard the cortex of the mesial wall of the reptilian hemisphere as partly homologous with the gyrus fornicatus, *i.e.*, with a pallial area. Yet both these writers speak with entire approval of the view that the dorsal commissure which springs from this mesial wall is the *psalterium* or hippocampal commissure. But if this mesial wall be partly gyrus fornicatus, its commissure must be corpus callosum.

A comparison of the reptilian cerebral hemisphere with that of the developing monotreme clearly demonstrates that the whole of the mesial wall of the reptilian hemisphere which is placed above the *pre-commissural body*, as well as a considerable part of the roof of the hemisphere, is unquestionably the homologue of

the hippocampus of the mammalian brain. Although the reptilian hippocampus is not so highly differentiated as its mammalian homologue, in that its margin is not yet definitely specialised to form the fascia dentata, yet we must utterly disagree with Kölliker in the statement that "das Ammonshorn nicht gebildet ist." The reptilian fornix springing from this hippocampus also contains representatives of most, if not all, of the groups of fibres which have been brought to light in the mammalia. From it springs the dorsal commissure or '*psalterium*.' It also includes representatives not only of the *fornix superior* of Koelliker, but also of his *fornix inferior*. It contains also pre- and post-commissural fibres, just as we have observed in the mammalia. The fornix is found also in the amphibia; and even in so lowly a vertebrate as *Petromyzon* we can still recognise a group of fibres connected with a dorsally placed cap of cortex, which must in all probability be regarded as the most primitive representative of the hippocampus.

ON THE NATURE OF THE WEIGERT-PAL METHOD.

By JOSEPH SHAW BOLTON, B.Sc., M.D., B.S. (Lond.),
*Demonstrator of Physiology in Mason University College,
Birmingham.*

I PROPOSE in this paper to state the results of an investigation into the nature of the Weigert-Pal 'medullary' stain, in which I have been engaged during the past six months. For a complete account of the development of the method of Weigert-Pal and of its modifications, I, from considerations of space, refer the reader to the well-known handbook of Bolles Lee.¹ Since the publication of the recent edition of this work, the only communication on the subject of any importance is a recent paper by Allerhand,² who recommends the use of liq. ferri sesquichlorati (50 p.c.), followed by a 20 p.c. solution of tannic acid which has been kept for some weeks, differentiation being performed by the method of Pal, using solutions of double strength.

The present investigation originated in a series of attempts to obtain Nissl's³ preparations from portions of a valuable hemisphere which had been placed in Müller's fluid four months previously. After numerous unsuccessful trials, which gave staining of little beyond the nuclei and the ground-substance, I attempted to similarly spoil formalin-hardened sections by treating them in various ways with solutions of the chromates, in order to determine, if possible, why in the chrome-hardened tissue the nerve cells refused to stain. On one occasion, on overstaining with methylene blue, soluble in water, and then transferring, after washing, to a 1 per cent. solution of ammonium bichromate, I noticed that the sections changed to a purple colour, and on then differentiating them with weak alum,

¹ *The Microtometist's Vade Mecum*, 4th ed., pp. 405-412.

² *Neurol. Centralb.*, 1897, p. 727.

³ *Neurol. Centralb.*, 1894, p. 508.

I was surprised to obtain what looked to the naked eye like purple Weigert-Pal specimens. On examining the sections under the microscope, however, I found that this appearance was due to a deposit of fine needle-shaped purple crystals along the course of the bundles of nerve fibrils. These crystals in a few minutes dissolved, the sections becoming of a diffuse blue colour. I then placed washed formalin-hardened sections, cut with a freezing microtome, without previous soaking of the block of tissue in gum, in a 1 per cent. solution of ammonium bichromate for a couple of days, and on then overstaining with methylene blue, and differentiating by the method of Pal, and also by simply washing out in absolute alcohol, obtained a blue Weigert-Pal result, partly composed of minute crystals and partly existing as a blue stain in the fibres. These results were also not permanent. I finally mordanted the sections for half an hour in an incubator at 40° C., in a .25 saturated solution of tannic acid, followed for a similar period by a bath containing 1 per cent. of tartar emetic, and then stained as usual with methylene blue, soluble in water, and differentiated by the method of Pal. This gave me typical Weigert-Pal results, the finest fibrils coming out a deep blue, and the result was permanent, though probably the deterioration which usually results when basic dyes are employed will eventually ensue.

As this method of obtaining the stain was simply the ordinary one used technically for the staining of woven fibres with basic dyes, I concluded that my result was due to an incomplete removal of the stain from fibres previously prepared to receive it, and, though exactly like a Weigert-Pal stain, was caused by the existence of *fibrils*, and was not necessarily dependent on the presence of a medullary sheath.

The consequent suggestion was that the Weigert-Pal process, instead of being a method of staining fine medullated fibres, might merely be a method of incomplete removal, by oxidation, of the mordant dye logwood, the parenchymatous part of the sections being naturally more readily permeable to the oxidising agent than the bundles of fibrils, and consequently more readily decolorised.

I have for upwards of a year extensively used a rapid modification of the Weigert-Pal method, which I believe to be original.

I have been accustomed to pass my sections directly from 5 p.c. formalin into Marchi's fluid, and then to warm them to 40° C. for half an hour, afterwards washing and warming in Kultschitzky's acid hæmatoxylin solution for an hour. By the use of half-strength Pal solutions I have become able, with practice, to obtain with certainty results histologically indistinguishable from those obtained by the slow method recommended by Schäfer.¹ Without experience, however, this method does not necessarily give the results desired. If the differentiation be done too rapidly and by a single immersion in permanganate, the result is a beautiful low-power specimen, with relatively coarse fibres and few of the finest fibrils. If, on the other hand, the differentiation be done more slowly, and particularly if the sections be several times transferred between the permanganate and sulphite baths, in order to wash away the precipitated manganese dioxide, the result is an exceedingly fine differentiation of the minute fibrils.

As a result of this observation, I quickly became convinced that the coarse fibres of rapid differentiation were simply cleaved bundles of finer fibrils, which would, by using a weaker bleaching solution, and by alternating the baths a few times, be differentiated into their elements.

Having, from this point of view also, developed a doubt as to the necessarily medullated nature of the fibres displayed by the Weigert-Pal method, I commenced a series of tests, employing 2 per cent. solutions of several metallic salts in place of the Müller's fluid and bichromate solutions that I had hitherto employed.

The tissue chiefly made use of was from the upper part of the right ascending parietal convolution of a healthy man aged 55 years, who had died of pneumonia, and it had been for six months in 5 per cent. formalin. The sections were cut in gum, without previous soaking of the blocks, by means of a freezing microtome.

The sections were in some cases dipped in 1 per cent. osmic acid, and in others left in the solution for 5 minutes. They were then warmed in the chosen metallic solution to 40° C. for half an hour, and afterwards washed and again warmed as

¹ *Essentials of Histology*, 3rd ed., page 297.

before for an hour in Kultschitzky's acid logwood. They were finally allowed to cool, and differentiated by the method of Pal. My results are as follows:—

Cobaltous Nitrate (6).¹—A jet-black staining of the fibres results, and the differentiation is excellent, the finest fibrils showing even to the surface of the cortex. The usual little varicosities of medullary tissue are apparent on the fibrils, both in the grey matter and in the superficial layer of this, and many exceedingly fine axis-cylinders exist, showing here and there a varicosity, these becoming more numerous during their downward course, till, when the bundles are reached, a definite agglomeration of the varicosities, and finally an obvious medullary sheath, appears. Thus in all respects these specimens are typical examples of the Weigert-Pal result in formalin-hardened cortex.

Cobaltous Nitrate (3).—Dipped in osmic acid. Colour a dirty purple. The differentiation is excellent, and the result is as good as in the last specimens, but the colour is so pale that the fibrils are difficult to follow readily.

Chrome Alum (4).—A perfect Weigert-Pal result. Fibrils jet-black and differentiation beautiful. In many cases an improvement on the cobaltous nitrate result, but perhaps accidentally only. An increase in the varicosity of the axis-cylinders as they are traced down. Upwards, the varicosity exists to the pyramidal layer of the cortex, but in some cases the appearance is lost altogether, and these specimens exhibit the typical wiry course seen in Golgi preparations. The varicosities are never jet-black like the axis-cylinders, but have rather the appearance of being most deeply stained at the circumference, and semi-stained elsewhere.

Iron Alum (7).—Is a typical result, and, taken generally, is perhaps an improvement on those from chrome alum. These specimens show additional points, owing to their less ready differentiation, such as an increased number of fibrils, many of which are medullated, and some coarsely so. Several axis-cylinders also are seen to pass into the superficial layer of the cortex, and occasionally a well-medullated fibre does the same.

¹ The numeral in each case refers to the number of specimens examined. In the majority of cases only one or two sections from each batch were preserved. Each specimen was invariably differentiated separately.

In some specimens, through more rapid differentiation, only medullated and varicose fibrils are evident, and in other parts the larger and deeper bundles are only partially separated into their individual fibres, or not at all. The larger fibres when seen in cross section, frequently appear as rings with a dark centre, due, as will be seen later, to a deep staining of the axis-cylinder, and a dark periphery, the substance of the medullary sheath being only partially stained.

Nickel Sulphate (2).—Is indistinguishable from the last specimens.

Copper Acetate (2).—Is also indistinguishable from the previous specimens.

Zinc Sulphate (2).—Dipped in osmic acid. These sections present the usual appearance, and exhibit very fine fibrillation, but are pale and semi-transparent compared with the preceding sets.

Manganese Sulphate (2).—Dipped in osmic acid. Is rather better than the zinc sulphate results, and would pass for a typical slow Weigert-Pal result.

Potash Alum (2).—Dipped in osmic acid. In parts is a typical result. In others the fibres are reddish, as if from a deficiency of osmic acid.

Citrate of Bismuth and Ammonia (2).—Dipped in osmic acid. Is slate-grey in colour, and the differentiation is not very good, owing to the transparency of the fibrils.

These remarkably constant results, with such dissimilar metallic salts, and with such an obvious explanation for the partial failures, at once led me to use osmic acid alone.

Osmic Acid (a) (2).—Dipped in 1 per cent. osmic acid, and then heated for 10 minutes in acid logwood. The result is an ordinary but pale Weigert-Pal preparation, with, however, the finest fibrillæ showing clearly. (b) (3).—Five minutes in 1 per cent. osmic acid, and heated for 20 minutes in acid logwood. The result is an average good Weigert-Pal specimen. (c) (4).—Five minutes in 1 per cent. osmic acid, and then for 12 hours in acid logwood in the cold. An ordinary Weigert-Pal result. The fibres are finer and more numerous than in the last set, and the differentiation was slower.

In a new series of sections from the same case, I next obtained

specimens by the rapid and slow osmic acid, and the slow osmic acid and chrome alum methods.

Rapid Osmic Acid (5).—Twenty minutes in 1 per cent. osmic acid, half an hour at 40° C. in acid logwood, and half-strength Pal solutions for differentiation. The result is a good Weigert-Pal set of specimens, with perfect differentiation to the finest fibrils. In many places these sections show thin axis-cylinders lying quite near to coarse medullated fibres.

Slow Osmic Acid (5).—Twenty minutes in 1 per cent. osmic acid, and 24 hours in acid logwood.

The sections are histologically indistinguishable from the last set.

Slow Osmic Acid and Chrome Alum (5).—Twenty minutes in 1 per cent. osmic acid, 24 hours in 1 per cent. chrome alum, and 24 hours in acid logwood.

The sections are histologically indistinguishable from the last two sets.

This result showed at least that the stain could be obtained as a pure osmic acid lake with hæmatoxylin, and not as a chrome-osmium lake; and in view of the fact that Weigert's original method involved the apparent formation of a copper-chrome lake, I proceeded to try the effect of most of the metallic salts at my disposal. I used these in 2 per cent. solutions, placed the sections in the chosen bath for 24 hours, and followed this by a bath of acid logwood, also lasting 24 hours. I afterwards differentiated by the method of Pal, using strengths of the solutions which I found best to suit the particular cases. I verified each of my results by performing at least two, and in many cases several applications of the entire process.

Ferric Chloride (2).—Colour dark blue-black of a transparent type, and not possessing the jet-black and partly opaque appearance of good osmium results. There is, however, perfect differentiation even to the finest fibrils, and the usual varicosities are present on these.

Zinc Sulphate (9).—Colour a very pale lilac, with in some sections a tinge of grey. The fibres are barely visible. The colour is very soluble in the differentiating fluids, and fades in a fortnight almost completely.

Manganese Sulphate (10).—Colour as in zinc sulphate results.

Is sometimes rather darker, and sometimes rather paler. Cannot be distinguished from the last set, either in appearance or stability.

Citrate of Bismuth and Ammonia (7).—Is less pale than the results of zinc and manganese. Colour, a pale grey-green. Very soluble, but many fine fibrils after several weeks are still visible. The extreme paleness of the fibres is the chief bar to their visibility.

Cobaltous Nitrate (17).—Colour purple, and less pale than that of the bismuth specimens. The differentiation is moderately good, but the fibrils are too pale to be seen readily, are easily washed out by reagents, and consequently tend to fade. They are visible several weeks after preparation.

Nickel Sulphate (9).—A much deeper purple than the cobalt result, and the differentiation is good. When finely differentiated, however, the fibres are too pale for practical use. Resembles the chromium result (see below). Does not intensify.

Iron Alum (15).—Is black. The differentiation is excellent, and quite equal to that of the ordinary Weigert-Pal preparation. The finest fibrils are brought out a deep blue-black with unusual clearness. Is permanent.

Chrome Alum (5).—The colour is purple, and of about the same depth as, or rather paler than, the nickel preparation. Is permanent, but is useless for practical purposes in comparison with iron and osmium, in spite of a moderately good differentiation.

Copper Sulphate (5).—Is purple. The differentiation is fairly good. It is better than the cobalt result, but not so good as the set after the use of nickel and chromium.

Potash Alum (9).—Is almost vermilion-red. The differentiation is as good as that from iron salts, and the colour is very agreeable. The finest fibrils are deep red, and perfectly clear. In both these and certain of the iron specimens the fibres look both clearer and finer under ordinary powers than do those in osmium preparations. The impression is somehow given by the preparations obtained from all the metals, excepting osmium, and in some cases iron, that the axis-cylinders are the parts chiefly stained.

If the potash alum sections be partially differentiated only,

whilst the fibres are not so clear, the cells are stained a beautiful red. If the sections be left too long in alum the nuclei of the glia cells and some of the nerve cells stain red, whilst the fibrils are not obvious. The satisfactory potash alum result is permanent, and, excepting for its red colour, is quite as good as an ordinary Weigert-Pal preparation.

Uranium Acetate (16).—Reddish purple fibres. The process of differentiation is slow, and many cells remain stained a dark lilac in some parts of the sections. The result is intermediate in many respects between those from nickel and chromium on the one hand, and from potash alum on the other. The blood in the capillaries, and also in places the nuclei of the latter, are well stained. Where the sections show good results, the fibres are very fine and clear, and contrast with the apparently coarser fibres of osmium preparations. The specimens gradually deteriorate on keeping, and the fibres become brownish, though they are still fairly distinct. The nerve cells, however, with the nuclei of the capillaries and of the glia cells, retain their deep lilac colour, and even apparently seem to increase it at the expense of the fibres. This result seems to occur when the tissue has been over-mordanted or placed in too strong a metallic bath, but I have not experimented further on this point.

Sodium Tungstate (8).—The result is almost the counterpart of that obtained by means of potash alum, excepting that the colour is a fairly deep slate-blue. There is better definition than in the chromium and nickel results, owing partly, possibly, to its slower differentiation, and many cells are beautifully stained. This result is also better and clearer than that from uranium, and even when over-differentiated the fibrils retain their clear and sharp appearance, and many large cells still retain their stain. The blood corpuscles in the vessels and many of the nuclei of the glia cells are stained nearly black. The fibrils seem very fine compared with those in osmium preparations. Although sodium tungstate specimens keep well, and in spite of the beautiful appearance exhibited by many of the bundles of axis-cylinders, the result as a whole is too pale for practical purposes.

Stannous Chloride (13).—The fibres in these specimens are stained a deep reddish-purple, and are well differentiated. The

excess of stain is moderately easily removed by ordinary Pal solutions, and if well washed in water after differentiation the sections pass safely through alcohol. If over-mordanted the sections are difficult to wash out. Good results are not obtained if the metallic bath be not made perfectly clear by the addition of the minimum quantity of hydrochloric acid that will do this at the time when the solution is prepared.

Ammonium Molybdate (18).—This bath gives a beautiful violet-blue result. The fibrils are deeply stained, and the differentiation is perfect. The sections bleach readily, and do not easily stain if treated with ordinary care. The colour is very agreeable, and the result is permanent.

Ammonia Alum (6).—The colour here is a brownish purple, and the result is very little better than that obtained from manganese or zinc. The differentiation is good, but the fibres are very pale, and consequently difficult to follow. The sections deteriorate very little on keeping.

I shall conclude my list of results by the addition of the following, which are of sufficient importance to merit separate notice, and have considerable indirect bearing on the nature of the Weigert-Pal process.

Tannic Acid, Tartar Emetic, and Methylene Blue (9).—These sections were placed in a quarter-saturated solution of tannic acid and heated to 40° C. for half an hour: they were then placed, after washing, for a similar period in a 1 per cent. solution of tartar emetic at 40° C.: and finally, after washing, were heated in a quarter per cent. solution of methylene blue, soluble in water, till bubbles appeared, and kept at this temperature for several minutes. They were then washed in water and differentiated by means of Pal solutions of double strength.

The result is in many places of the typical Weigert-Pal type, the fibrils, large and small, being stained a deep blue, and exhibiting great clearness and very good differentiation. There has been little or no deterioration in these specimens since their preparation.

Kidney of Dog (cut by freezing).—

(a) *Ordinary Slow Osmium Method* (5).—The result is a beautiful low-power specimen. Some tubules, especially the loops of Henle, excepting when they have been cut into, are jet-

black, whilst others, chiefly the convoluted tubules, are greyish black. The medullary tubules are hardly stained at all, and the glomeruli and the tubules entering them not at all. Under a high power the result is seen to be due to a simple washing-out process.

(b) *Slow Iron Alum Process* (6).—Exactly the same result, excepting that the parts stained possess a purple-black colour instead of a genuine black.

Liver of Pig (frozen sections).—

Slow Osmium, and also Slow Iron Alum Process (4).—The differentiation here, as might be expected, occurs evenly all over the sections, and they are finally left practically unstained.

Muscular Coat of Small Intestine of Roach (formalin-hardened).—

Slow Ammonium Molybdate Process (1).—Under differentiation the bundles of circular muscle fibres gradually clear up, then separate into individual deep blue fibres, and finally, if the process continue, are completely washed out.

Cerebral Cortex from a General Paralytic. (Right paracentral region. Six weeks in formalin.)—

(a) *Rapid Osmic Acid Process* (10).—Result black, many coarsely medullated fibres and relatively few fine fibrils. The blood corpuscles, with which the vessels are congested, are stained a jet-black even in the fine capillaries. Many nucleoli remain stained in the larger nerve cells. Differentiation is excellent from a coarse point of view, and there are many varicosities on the fibrils.

(b) *Slow Osmic Acid Process* (5).—The differentiation was carried out as slowly and carefully as possible. The resulting specimens show many more fine varicose fibrils than are to be seen in the previous set, but even here very few bare axis-cylinders are visible. The vessels are washed out much more than is the case in the previous preparations, and the nucleoli of the nerve cells have disappeared. Many varicose medullated fibres exist in the superficial layer of the cortex.

(c) *Slow Iron Alum Process* (7).—A very perfect result. Numerous coarse and fine fibrils, the former medullated and the latter varicose, are visible, but the fibrils all seem shorter than is usual, and also more tortuous. The black staining of the congested blood-vessels is, however, the marked feature in

the specimens, and for my present purpose is the only important one.

I finally completed my study of the Weigert-Pal process by making a careful examination of my variously-prepared sections under magnifying powers of from 1000 to 1500 diameters and soon obtained a satisfactory termination to my investigation by this means.

I have already referred to the varicosities of myelin which exist on the cortical fibrils when the sections are prepared by

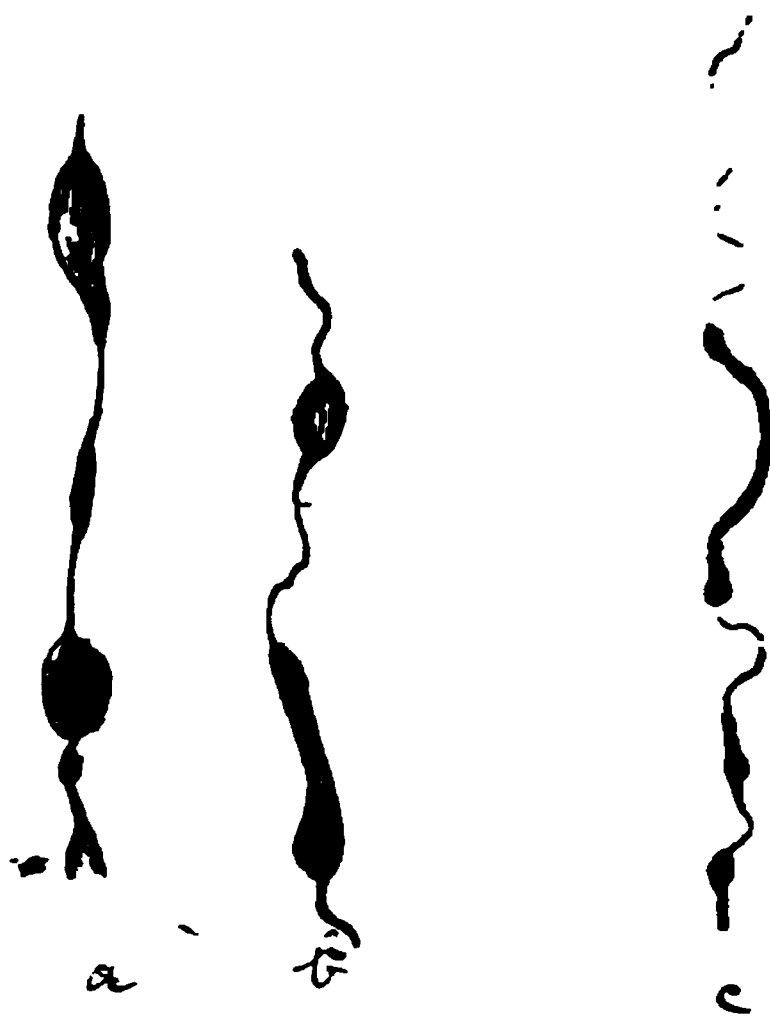


FIG. 1.—*a* and *b*, terminal axis-cylinders with varicosities of myelin attached to them. Osmic acid specimen. *c*, another terminal axis-cylinder, assuming the usual wiry appearance on getting free from its medullated sheath. [Zeiss apochromatic water-immersion. Eye-piece No. 18 ; draw-tube 160 mm.]

the method I have adopted. I have also stated that I gained a general impression, when using the ordinary powers, that the fibrils in the preparations made from most of the metallic salts were finer than those obtained by the use of osmium. Under a Zeiss apochromatic water-immersion, with eye-piece No. 18 and the draw-tube at 160 mm., it at once became evident that the varicosities were really lumps of myelin, and also that the axis-cylinders themselves were deeply stained with the dye. Fig 1

shows the appearance of the terminal axis-cylinders in an osmic acid specimen before the myelin has entirely left the fibril. In these specimens both the axis-cylinder itself and the remains of the medullary sheath are stained deeply. Fig. 3, on the other hand, represents the appearance of the corresponding objects when sodium tungstate is used as a mordant; and here the axis-cylinder is stained a deep blue-black, whilst the medullary sheath

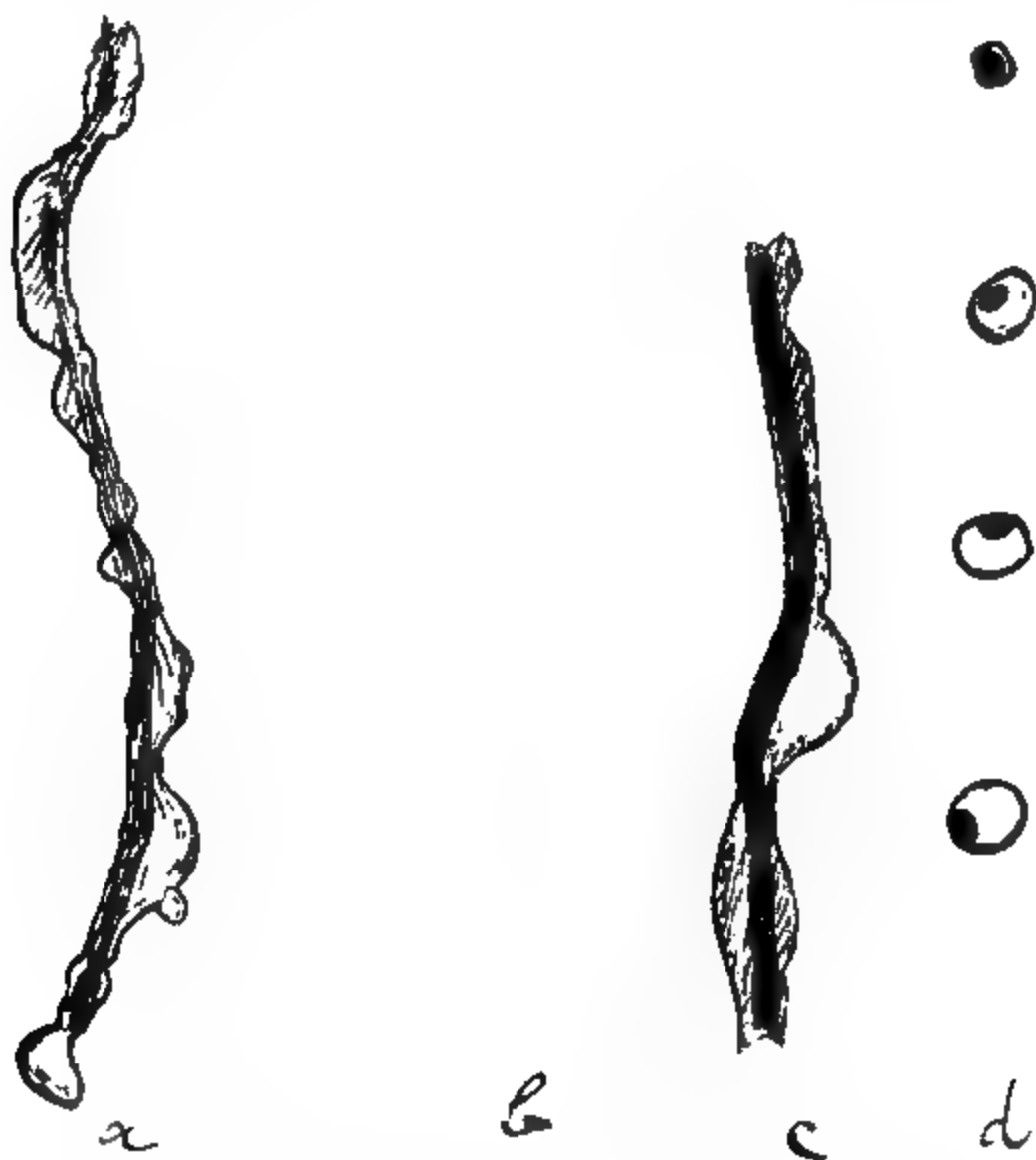


FIG. 2.—*a*, *b*, and *c*, nerve fibres as they enter the grey matter, showing the stained axis-cylinder inside the irregularly varicose medullated sheath. Chrome alum and osmic acid specimens. *d*, transverse sections of similar fibres. [The same magnification.]

is quite unstained, and can only be discerned owing to its high power of refraction. The intermediate condition between these two extremes is shown in fig. 2, taken from a chrome-alum-osmium specimen, where both the axis-cylinder and the medul-

lary sheath are stained; but the former is so much deeper in colour that it is clearly visible both in the ordinary fibres, fig. 2, *a*, *b*, and *c*, and in the cross-sections, fig. 2, *d*.

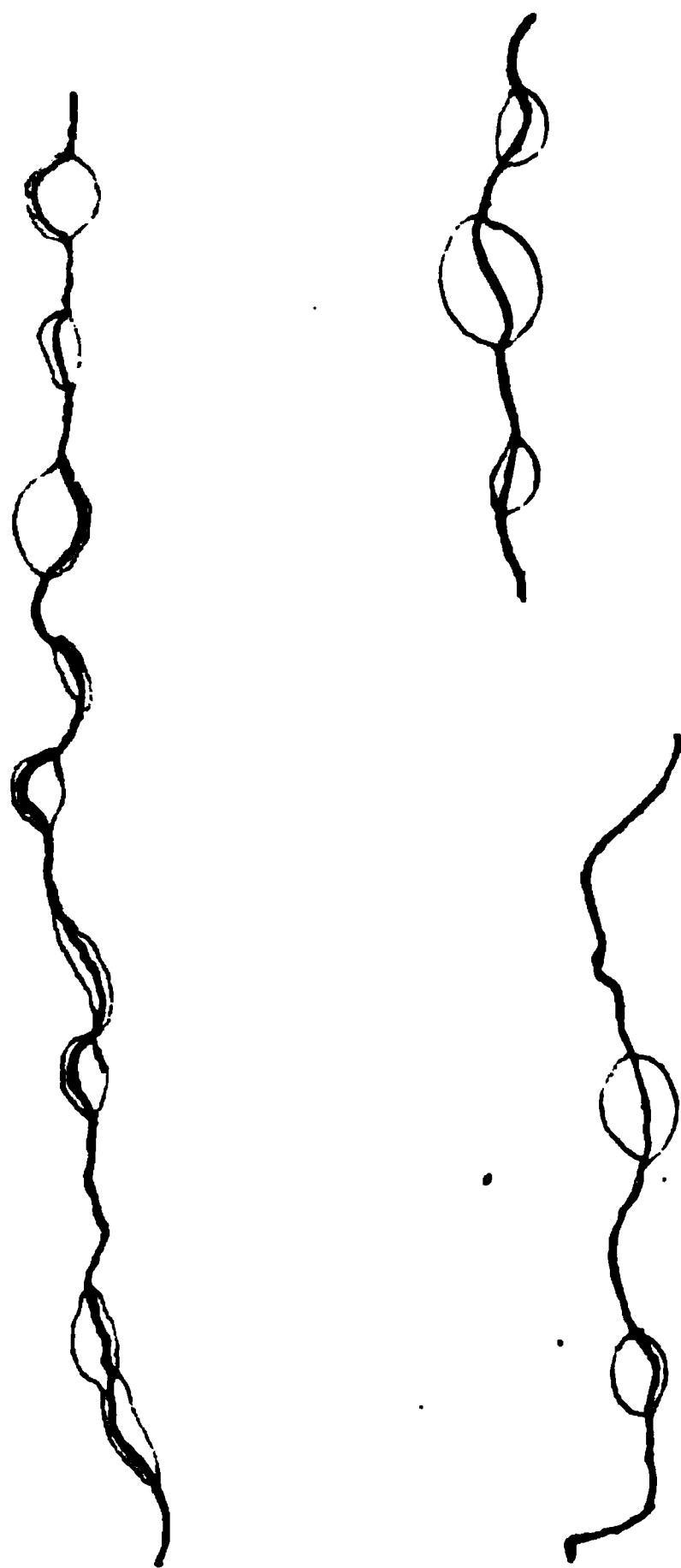


FIG. 3.—Varicose terminal axis-cylinders from a sodium tungstate specimen, in which the myelin is quite unstained. [The same magnification.]

Between the two extremes represented in figures 1 and 3, all degrees exist. For example, iron alum resembles osmium in causing a deep staining of the medullary sheath, which usually

completely hides the axis-cylinder, though in both these cases, with care, the latter can usually be detected in at least a few fibres. Tin chloride stains the axis-cylinder a violet colour, and the medullary sheath a pale pink. Ammonium molybdate stains the axis-cylinder a deep slate-blue colour, and the medullary sheath a pale blue. Uranium acetate, potash alum and doubly mordanted methylene blue resemble sodium tungstate in leaving the medullary sheath practically unstained, whilst they stain the axis-cylinder respectively a deep purple, red, and blue colour.

Hence, the Weigert-Pal process is not a specific method for the staining of medullated nerve fibres with hæmatoxylin, but is a method of dyeing fibrils which comprises three distinct operations: the mordanting of the fibrils, the formation of a lake in them, and finally, the removal of the stain by oxidation from nearly every other part of the complex tissue under treatment.

The lake, as in the case of the osmium, and usually of the iron compound, may stain the medullary sheath, when it exists, as well as the axis-cylinder, and to such an extent that the two cannot be distinguished. It may, on the other hand, whilst it deeply stains the axis-cylinder, scarcely stain the medullary sheath at all, as in the cases of the logwood lakes of sodium tungstate, uranium acetate, and potash alum, and of the doubly mordanted methylene-blue lake. It may, finally, moderately stain the medullary sheath, and deeply stain the axis-cylinder, as in case of the stannous chloride and ammonium molybdate logwood lakes.

The various lakes studied during this research may be classified into three groups, as follows:—

CLASSIFICATION OF LAKES.

GROUP I.—*Of practical value.*

The logwood lakes of osmic acid, iron alum, ammonium molybdate, and ferric chloride.

GROUP II.—*Of more purely theoretical value.*

- a. The logwood lakes of stannous chloride, sodium tungstate, uranium acetate, and potash alum.
- b. The doubly-mordanted methylene-blue lake.

GROUP III.—Of relatively little value, owing to their faint colour.

The logwood lakes of nickel sulphate, chrome alum and the chromates, copper acetate, cobalt nitrate, citrate of bismuth and ammonia, ammonia alum, manganese sulphate and zinc sulphate.

This explanation of the nature of the Weigert-Pal process being accepted, it may not unnaturally be asked whether the fibres of other tissues can be similarly stained; and if not, why? In reply to this by no means improbable suggestion, I wish to advance the following considerations. Hæmatoxylin, like other stains of its class, is most intensely deposited in the parts of the tissue possessing the greatest actual or potential metabolism. Such tissues as the fibrous and the elastic, and the various fibrillated matrices, though they readily stain with certain 'general' stains, do not easily stain with any of the 'special' stains, owing probably to their stable and perhaps impervious structure. The only tissue in the body possessing minute fibrils of considerable length, and also of high potential, though possibly low actual, metabolism, is that composing the essential part of the nervous system; and it is consequently here, and here alone, that the Weigert-Pal method has a suitable field for its operation on a minute scale. On a relatively large scale, however, the method is equally applicable elsewhere. For example, the kidney, as I have already shown, presents, under a low power, a beautiful appearance after being submitted to the Weigert-Pal process. The fact that the fibres of the kidney substance are minute tubes affects all its parts equally, and neither causes nor tends to prevent the beautiful differentiation which results from the application of the method. It is, of course, as a washed-out specimen, of as little value when seen under a high power as would be a Weigert-Pal specimen of cerebral cortex if the fibres were magnified to the same size. Again, if the involuntary fibres in the circular muscular coat of the intestine of the roach be over-stained in acid logwood after mordanting with ammonium molybdate, on differentiating by the method of Pal they exhibit a beautiful low-power appearance, becoming visible first as groups and later on as single fibres, after which, if the process be continued, they decolorise. Organs generally parenchymatous in structure, such as the liver, as might be expected, either remain black or de-

colorise entirely, according to the degree to which the bleaching is carried out. Lastly, the blood corpuscles in engorged vessels readily mordant and stain, and with difficulty decolorise; also the nucleolus of the larger nerve cells frequently remains black, even when over-differentiation has been performed and many of the finer fibrils are washed out.

Thus the Weigert-Pal process generally, compared with that of technical dyeing, is on a microscopic scale, and is performed on a complex structure. Just as fine glass threads included in a web would not stain, so nearly the whole of the fibres in the body, excepting those belonging to the neurons, do not stain, owing to the fact that they refuse the mordant, and consequently the lake. This principle receives an illustration from the methods of hardening in common use; for whereas it can be laid down as a broad rule that some chrome compound is desirable as a hardening agent for many of the protoplasmic tissues, it is an equally broad rule that alcohol is usually advisable when the fixing of the connective tissues and of many neoplasms is required; that is, when desiccation and preservation only are necessary. The usual unwelcome exception which tests our rules here appears in the form of the softer glands, which are usually hardened in alcohol. The explanation of this exception is, however, that these particular tissues, to be preserved at all without disorganisation, must be rapidly fixed, chiefly by coagulation and desiccation.

I have during this research made use of tissue which had been rapidly killed by and then preserved in formalin, thus avoiding any undue tampering with the tissue elements; this being the special property of this valuable reagent. I have also experimented with human cortex cerebri only, as this tissue has for some time past been my especial study, but my explanation of the Weigert-Pal process can equally be applied to other parts of the nervous system. It requires careful differentiation and thin sections to bring out the individual medullated fibres in a section of spinal cord, ganglion or nerve, and the ring-shaped appearance of transverse sections of the medullated fibres is easily explicable if one supposes that the stain, as is probable, is more easily washed out from the axis-cylinder fibrils than from the denser medullated sheath, which, as I have shown, is intensely stained in osmium, and usually also in iron preparations. The fine collaterals in the

grey matter of the spinal cord are, as in the case of the fibrils of the cerebral cortex, at least a hundred times smaller in section than an ordinary medullated fibre. These fine fibrils are easily decolorised in sections of spinal cord which are not sufficiently thin, long before the coarse fibres of the white matter are differentiated, owing to the fact that they more frequently run separately than in bundles, such as are seen in the cerebral cortex. The analogous part of the latter is rather the superficial half of the grey matter, after the sheaves of fibrils have separated into their elements. Especially in under-differentiated parts of the cortical grey matter, a more or less inter-communicating mesh-work, with nodes occasionally, exists here and there, owing probably to the fact that portions of stain remain where certain of the fibrils nearly approach one another; and this is, in my opinion, one cause of the difference in appearance between Weigert-Pal and fibrillar Golgi preparations. No nodes occur in the latter, as the chromate of silver is deposited in the fibrils, or in their canaliculi; whereas in the former they are not rare, as might be expected, when such a coarse method as that of differentiation by bleaching is employed. Occasionally small thickenings, apparently due to incomplete washing out, exist on the terminal axis-cylinders at the proximal and distal ends of certain of the varicosities of Myelin. These constitute the only evidence I can adduce in favour of the existence of a thin homogeneous primitive sheath. They are, however, susceptible of a more obvious interpretation, and I am personally inclined to doubt the presence of such a sheath. As far as I am able to judge from comparison, there is little or no difference in size between the properly differentiated Weigert-Pal axis-cylinders in the cortex, and the fibrils brought into view during the chrome-silver impregnation of formalin-hardened brain. These are especially numerous, and are presumably nervous in nature, in general paralysis, but occur to a greater or less extent in all cases after about a week's immersion in the chrome bath. I will not refer further here to this subject, as I have a paper in course of preparation, in which I hope to deal with the matter more fully.

As I stated at the commencement of this paper, a method has been recently introduced by Allerhand, which consists in the impregnation of chrome- or alcohol-hardened preparations with a

black tannate of iron, the sections being differentiated in Pal solutions of double strength. This method explains the jet-black coloration I obtain with iron alum and logwood, as the latter contains tannin, and it enables one to dispense with a dye. The chief objection, probably, to a sufficient trial of the method of Allerhand, is the fact that the tannin solution takes so long to prepare, whilst the question of its cheapness, which its originator especially emphasizes, will be of little interest to most neurologists, owing to the relatively small quantities of the reagents which are employed.

METHOD.

The following method, which in my hands gives very satisfactory results, seems to be the natural outcome of the present investigation. The sections, preferably cut by the freezing method, and without any soaking of the blocks in gum if they be formalin-hardened, should be mordanted for a few minutes, till the white matter becomes fawn-coloured, in a 1 per cent. solution of osmic acid, or for a few hours in a 2 per cent. solution of iron alum or of ammonium molybdate. The latter bath may be hastened by placing the sections in an incubator at 40° C. They should then, after washing, be stained for some hours in the cold, or for about two hours in an incubator at 40° C. in acid logwood, and after again washing, they may be bleached by the method of Pal. The most perfect results are obtained by at first leaving the sections for a few seconds only in the permanganate solution, and by alternating the bleaching-baths till, as experience only can teach, differentiation is completed. They should afterwards be washed in distilled water, mopped dry on a lifter with blotting-paper, and transferred directly to absolute alcohol for a few seconds. They should then be again mopped dry and placed in chloroform, which will float them out if any shrinking, which is unusual in my hands, has occurred, and should finally be passed into xylol without mopping, and mounted in moderately fluid xylol balsam. I usually, without any injury to the sections or any deposition of fibres, dry my sections by pressing clean blotting-paper on them before applying the balsam.

If the sections are brittle, they have been left too long in the

acid logwood. The preparations are best differentiated by using a number of porcelain dishes and pouring the various fluids over them and away from them, this dispensing with a considerable amount of handling, and consequent possible injury. If the sections are left too long in alcohol or under-washed in distilled water after differentiation, some dissolving out of the stain occurs. Chloroform to some extent prevents this from continuing, and it mixes with a trace more water than does xylol, whilst it also at once completely flattens out the sections, without any liability to injury from diffusion currents if the alcohol be mopped off before they are placed in it.

CONCLUSIONS.

1. The Weigert-Pal process consists in the incomplete oxidation of a stain from mordanted fibrils containing it as a lake, and bears no necessary relation to the occasional presence of a medullary sheath round these.

2. If an ordinary mordant dye such as logwood be used, a metallic salt, to mordant the fibres previously, is necessary.

3. If a basic dye, such as methylene blue, soluble in water, be used, double mordanting with tannic acid, and afterwards with tartar emetic, is necessary.

4. The ordinary Weigert-Pal result can be obtained by the use of osmic acid alone, as this forms a jet-black lake with hæmatoxylin in the absence of other metals.

5. Almost as good or equally good results can be obtained by the use of 2 per cent. solutions of iron alum, ammonium molybdate, ferric chloride, stannous chloride, sodium tungstate, uranium acetate, and potash alum; and much inferior results, arranged in order of value, can be obtained by the use of similar solutions of nickel sulphate, chrome alum and the chromates, copper acetate, cobalt nitrate, citrate of bismuth and ammonia, ammonia alum, manganese sulphate, and zinc sulphate.

6. Osmic acid and usually iron alum cause a practically equal staining of the medullary sheath and of the axis-cylinder, whilst the other metals chiefly cause staining of the axis-cylinder, the medullary sheath being either slightly stained or quite unstained, according to the metal employed.

7. A lessened rapidity of differentiation, and particularly an alternate use of the permanganate and sulphite baths, to remove the precipitated manganese dioxide, greatly increase the fineness of the differentiation.

8. The non-correspondence of osmium-chrome-logwood and Golgi results is thus readily explicable.

I desire, in conclusion, to express my indebtedness to Dr Powell White, of the General Hospital, Birmingham, and to Dr Wigglesworth and Dr A. W. Campbell, of the County Asylum, Rainhill, for the material used in this research; also to Drs Baker and Innes, and especially to Professor F. J. Allen, of Mason College, for many valuable suggestions and criticisms.

SKULL OF AN ADULT MICROCEPHALIC IDIOT. By
the Rev. F. C. KEMPSON, M.B., Gonville and Caius College,
Cambridge, *Demonstrator of Anatomy, Cambridge University.*

THE present skull is of unknown age, and without a history: it was found on a shelf in a provincial hospital, where it seems to have lain for many years. It is obviously a case of congenital microcephaly, similar to the case of "Joe" described by Professor Cunningham and Dr Telford Smith in the *Scientific Transactions of the Royal Dublin Society* (vol. v. series ii. p. 339). The microcephaly of the present skull is not quite so extreme as in the case described by Professor Cunningham.

The leading features of the present skull are—

- (1) The absence of simian characters, especially in the face, except as regards curvatures and proportions.
- (2) The absence of any trace of injury or disease.
- (3) The disproportion between cranium and face, the former being diminutive, the latter of almost normal size.
- (4) The small size of some of the foramina at the base.
- (5) The absence of synostosis in the cranial sutures, except the sagittal.

These facts point to microcephaly of the cranium being secondary to arrested cerebral development; so that while the brain may probably have presented atavistic characters, yet such peculiarities of the skull as might be called simian are only so accidentally, and arise out of the necessary changes in curvature involved in adapting a diminutive calvarium to a basis cranii of almost normal size. The mandible is missing.

There is no marked peculiarity in the face. The vertical depth from nasion to alveolar point is a little below the average, and the face is also somewhat narrow and pinched. The palate is narrow and oblong, almost hypseloid, but is not deeply vaulted, and is without any trace of deficiency. This narrowness may be due to the loss of the molar teeth, whose alveoli are almost all obliterated.

ated, and the alveolar processes are shrunken. The nose is very prominent, the projection being due to the prominence of the angle between the anterior margin of the nasal process and the body of the maxilla, the nasal bones being normal: the orbits are also of about normal size. The glabella is very prominent and rounded, and is continued laterally into the superciliary eminences which extend outwards no farther than the faintly marked supra-orbital notches; from this point to the external angular process the upper margins of the orbit form a thin, prominent crest. The zygomatic arches are shorter and the passages under them smaller than usual, but they are as thick as in an ordinary male

FIG. 1. — *Norma facialis*.

skull, and therefore of relatively greater strength. The temporal ridges are really face characters, their position being dependent on the size of the temporal muscle; they are at the normal height above the zygoma, and indicate temporal muscles of normal size in agreement with the other structures of the face, but the cranium being so small, there is but a small distance (about 35 mm.) between the temporal ridges and the sagittal suture, and this gives them the appearance of being placed unusually high.

The greatest transverse diameter of the cranium is through the mastoid processes, and the greatest longitudinal is from the

glabella to the external occipital protuberance. This latter prominence is of unusual size. The longitudinal diameter, from the glabella to the point on the occipital bone, which is normally the greatest diameter, is slightly less than the maximum longitudinal diameter; while the transverse diameter through the back part of the squamous bones, which is usually the maximum, is very considerably less than that through the mastoids; and it would seem that a truer cephalic index for comparison with normal skulls will be obtained from these measurements than from those. The calvarium is diminutive, but otherwise normal, except in so far as its curvatures are altered by being placed on



FIG. 2.—Norma lateralis.

a basis cranii of normal dimensions. There is no synostosis in any of the sutures except the sagittal, and there it is incomplete. The base of the skull presents a fairly normal appearance. The mastoids and external occipital protuberance are exceptionally prominent; the condyles are on a lower plane than the mastoid process, and are completely visible in a side view of the skull. The external auditory meatus is short, and the outer end of the tympanic bone directed downwards, as in the case described by Professor Cunningham. The foramen magnum is large, of full normal size; of the other foramina, the carotid and jugular are very decidedly small, the latter also directed forwards to an

unusual degree, and the jugular fossa is very small. The foramen ovale is small, and almost circular. The anterior condylar foramina are unusually large.

The form of skull suggests a brain similar to those described by Professor Cunningham, with full-sized basal portions, and cerebral hemispheres ill developed, especially in the occipital and frontal regions. It is instructive as indicating how little

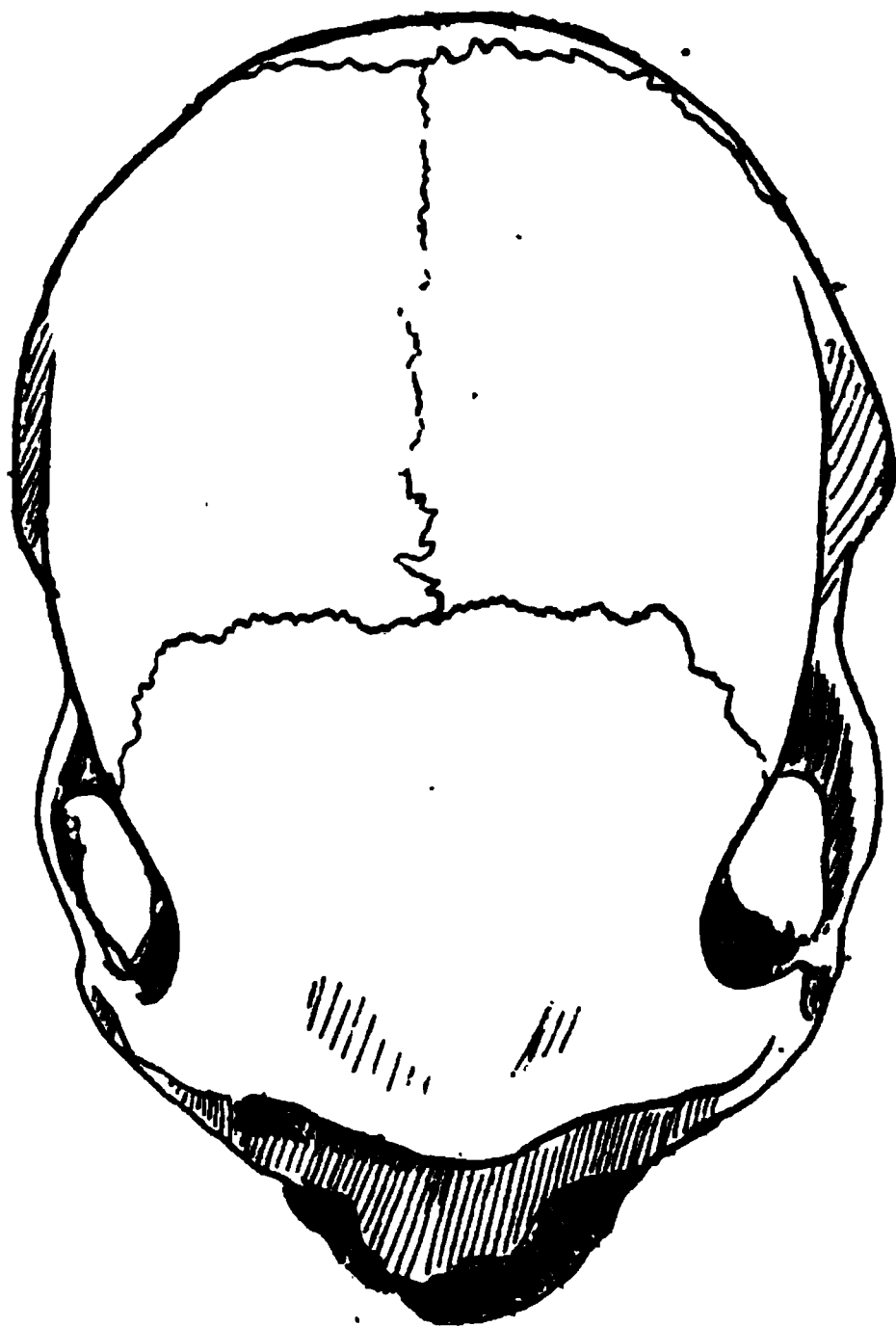


FIG. 3.—Norma verticalis.

one can predicate the prognathism or other characters of the face from the slope of the brows and brain case.

The measurements are as follows:—

Greatest length, *i.e.*, from glabella to external occipital protuberance, 162 mm.

Greatest breadth, *i.e.*, between mastoid processes, 121 mm.

Length, corresponding to maximum length of normal skull, 156 mm.

Breadth at usual point of greatest breadth, 103 mm.

Biorbital width, 95 mm. (*N.B.*—The skull is so narrow here that the zygomata can be seen from above.)

Basi-nasal length, 94 mm.

Basi-alveolar length, 92 mm.

Superior facial height, 67 mm.

Least frontal width, 76 mm.

Bistephanic width, 65 mm.

Biasterial width, 105 mm.

Biauricular width, 95 mm.

Bizygomatic diameter, 112 mm.

Nasal height, 49 mm.

Transverse diameter of nasal aperture, 22 mm.

Basio-bregmatic height, 108 mm.

Capacity in c.cm., 650.

Indices

Cranial, from maximum dimensions, 74·7.

Ditto, from measurements between usual points, 66.

Gnathic, 98·7.

Nasal, 44·9.

The outlines of the accompanying figures have been taken with the stereograph. They have been reduced by photography to about half scale.

**THE MORPHOLOGY OF THE TRIANGULAR CARTILAGE
OF THE WRIST. By EDRED M. CORNER, B.A., B.Sc.,
Sidney Sussex College, Cambridge.**

THE triangular fibro-cartilage of the wrist may be one of two things,—a carpal element, or a modified portion of the capsule of the joint which has undergone specialisation. In the following notes I believe that the evidence which I have collected indicates that this structure, in a sense, is both—that it is built on a vanished carpal element; but that this structure, as it appears in the adult, is mainly derived from the capsule of the joint.

Owing to the various positions assumed by the elements entering into these joints in different animals, I have used the terms flexor or palmar, extensor, radial or ulnar, for anterior posterior, external, and internal respectively. I have examined the wrist joints in the following types:—tortoise, ox, sheep, pig, dog, cat, monkey (*cercopithecus*), and man, both adult and foetal. Of all these, the simplest form of joint is that of the tortoise, in which both the radius and ulna participate about equally, articulating directly with the proximal row of the carpal bones. The modifications shown in the other types are correlated with variations in the function of the forelimb as regards weight-bearing, rotation, or amount of flexion. When the first of these functions predominates, the radius becomes relatively larger than the ulna; and with the acquisition of the power of pronation and supination, considerable changes take place in the arrangements of the ligaments. The modifications in the wrist in each of these cases is related to corresponding changes in the elbow.

The ox's wrist illustrates the modification for weight-bearing. The ulna does not enter into the joint; and although this bone reaches the wrist in the sheep and pig, yet its presence has not materially affected the arrangements of the ligaments. In none of these animals is there any trace of a triangular fibro-cartilage. In the wrist of the dog there is a slight amount of rotation permitted. When the joint is opened on its extensor side (fig. 2).

two ligaments are conspicuous on account of their cruciform arrangements.

1. A short radio-carpal ligament (*r.c.*), arising from a ridge on the ulnar side of the middle of the flexor surface of the radius, and inserted on the flexor aspect between the scapho-lunar and the cuneiform bones.

2. An ulno-carpal ligament (*u.c.*) from the flexor surface of the ulna at the base of the styloid process to the palmar surface of the scapho-lunar bone. A slip of this ligament goes on to the trapezium.

The triangular cartilage is present in this joint (figs. 1 and 2, *t.c.*). Its structure is mainly fibrous; and it is attached to the extensor edge of the radius on the ulnar side, and to the lower lip of the sigmoid facet of the same bone. Its flexor border is semi-lunar and free; its extensor edge is closely connected with the extensor ligament of the wrist.

In the cat (fig. 3), a still greater amount of rotation can take

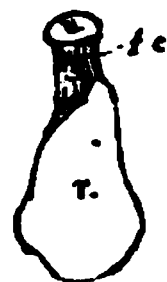


FIG. 1.—Dog's wrist. Surfaces of radius and triangular cartilage seen from below; *r.*, radius; *u.*, ulna; *t.c.*, triangular cartilage.

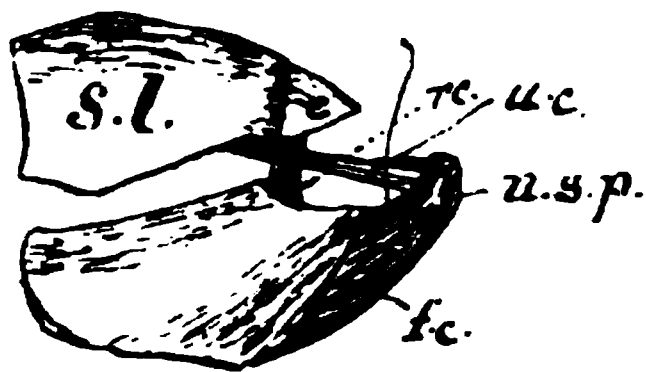


FIG. 2.—Dog's wrist, opened from behind; *s.l.*, scapho-lunar bone; *t.c.*, triangular cartilage.

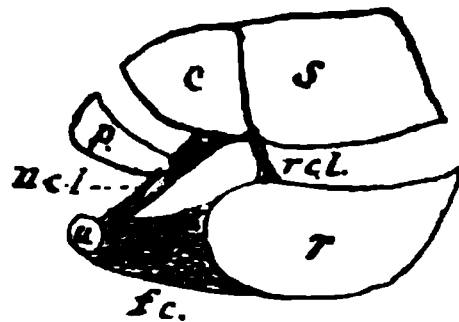


FIG. 3.—Cat's wrist, opened from behind; *p.*, pisiform; other letters as before.

place, and the structures in the joint show the following arrangements:—

1. The radio-carpal ligament (*r.c.*) is smaller than in the dog.
2. The ulno-carpal ligament (*u.c.*) is connected with the pisiform bone which enters into the wrist joint, but its other attachments are as in the dog.

The triangular cartilage (*t.c.*) is larger than in the dog, and has similar attachments, but its flexor edge is also attached to the capsule near the styloid process of the ulna.

In the monkey (fig. 4), pronation and supination are freer than in the preceding types, and the styloid process does not articulate with the cuneiform or pisiform bones, as it does in them. The ligaments are as follows:—

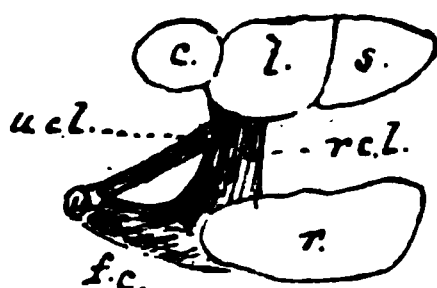


FIG. 4.—Monkey's wrist from behind.

1. The radio-carpal band is as in the cat, but a part of it is inserted into the radial third of the flexor edge of the triangular cartilage.

2. The ulno-carpal ligament arises from the base of the styloid process, and is inserted into the palmar surface of the semilunar bone.

The triangular cartilage (*f.c.*) is attached as in the cat, but has a smaller attachment to the extensor edge of the radius, its extensor margin being attached to the corresponding part of the capsule. Its flexor edge is attached to the ulno-carpal ligament near the base of the styloid process, and to the radio-carpal ligament near the radius. These ligaments have been described by Mr Arthur Keith in this *Journal*, vol. xxviii. p. 149.

In the human wrist, in which pronation and supination are more perfectly capable of taking place, the following points are noticeable:—

1. The radio-carpal ligament is as in the monkey; but its radial attachment is very small, and it is mostly connected with the flexor edge of the triangular cartilage.

2. The ulno-carpal ligament is fused with the cartilage, from which it can only be separated by an artificial dissection. This ligament can be seen in sections of the foetal wrist. The fibro-cartilage in man is intimately attached both to the flexor and to the extensor parts of the capsule.

Mr Keith has described the ulno-lunar ligament as absent in man: it is really present, but inclosed in tough fibro-cartilaginous tissue. I have, however, seen it much more distinct, and easily separable.

Professor Leboucq of Ghent, in his papers on the morphology of the carpus,¹ has described the development of the triangular

¹ *Bulletin del' Academie royale des Sciences de Belgique*, T. iv., No. 8, p. 170, 1882; *Archives de Biologie*, T. v., p. 35, 1884; *Anatomischer Anzeiger*, 1886, p. 17.

cartilage. The first trace which he finds is a cartilaginous nodule (fig. 5, *ca.*) in a band of tissue joining the styloid process of the ulna with the semilunar bone (*L.*). This is present in the fetus of the 3rd and 4th months, but disappears later. The band of tissue in which this nodule is developed is also attached to the lower end of the radius, and its attachment to the semi-

ca....



FIG. 5.—Section of wrist of a third-month fetus, showing the temporary cartilage (*ca.*).

FIG. 6.—Section of wrist in a fourth-month fetus.

lunar bone disappears later. He considers this nodule to represent the proximal extremity of the pisiform digit of Gegenbaur and Wiedersheim, and to be intercalated between the ulna and the cuneiform on the palmar side.

The sections which I have made are in exact accord with Professor Leboncq's description (see figs. 5, 7, and 8). The nodule which is distinct in the fetus of the fourth month is not recognisable in the fifth month, and by that time also the band

- *ca.*



FIG. 7.—Section of wrist in a fourth-month fetus, showing the temporary cartilage (*ca.*).

FIG. 8.—Fifth-month fetal wrist; the cartilage has disappeared.

connecting the semilunar to the ulnar styloid has disappeared, except at the radial palmar part.

By comparing serial sections of the wrist at the fifth month the ulno-carpal ligament can be distinctly isolated, passing from the styloid process to the semilunar bone; also its radial attachment is extremely thin at its central part.

Summing up the deductions which may be drawn from these observations, it appears that we must ascribe a double origin to this structure. Its first germ was probably the rudimentary carpal element of the vestigial pisiform digit: this only accounts for a very small part, if any, of the structure which survives in the adult, by far the larger part of which is derived from the articular capsule. The lower radio-ulnar joint is a sort of swivel, around which fasciculi of the capsular ligament are arranged, attached to the styloid process. As the capacity for rotation develops, these fascicles are dragged into the joint both from the flexor and from the extensor side. These elements are sometimes unequally developed, as in the dog, in which, on account of the flexor-ward twist of the styloid process, the cartilage is especially connected to the extensor side, and is free on the flexor side. In the small series which I have examined,



FIG. 9.—Palmar part of fifth-month fetus. Origin of u.c.l. is not in section.

the gradual absorption of the two ligamentous bands is well illustrated.

This double nature of the fibro-cartilage suggests an explanation of the cases of perforation of the cartilage occasionally met with. Professor Shepherd of Montreal notes that the perforation is frequently pathological, but it also occurs in healthy joints (see this *Journal*, vol. xxv. p. 349). It has been noticed that the structure of this element varies in different situations, being more purely cartilaginous at its radial attachment, and more purely fibrous towards its margins (Morris, *Anatomy of Joints*, p. 263). The fact of the articulation of the semilunar bone with the cartilage is mentioned in few text-books, although sometimes figured. This has been referred to by Professor Shepherd. My sections show that in the third and fourth months the cartilaginous semilunar articulated with the radius

only, and does not touch the triangular cartilage until the fifth month (figs. 6 and 8).

The elements which thus appear to make up this structure are—(1) the two bands of the capsule interjected into the joint as its capacity for rotation increases, and (2) between them the vestigial tissue which once indicated the existence of the carpal element of the vanished ulnar digit.

3 THYMUS GLAND IN THE MARSUPIALIA.¹ By
JOHNSON SYMINGTON, M.D., *Professor of Anatomy, Queen's
College, Belfast.*

In the year 1845 John Simon published a work entitled *Anatomical Essay on the Thymus Gland*, which contained a chapter specially devoted to the comparative anatomy of this organ. Previous to his researches, the view that the thymus was absent in the marsupialia had been maintained by such authorities as Vicq-d-Azyr, de Blainville, and R. Owen; and even in 1871 Ley, in his *Anatomy of Vertebrated Animals*, when describing the characters of the didelphian group of mammals, wrote: "the foetus is said to possess a large umbilical sac . . . and to be devoid of a thymus gland" (p. 280). Simon, however, found that he believed to be a thymus or its remains in the following members of this group of mammals, viz., *Didelphys opossum*, *Perameles obesus*, *Phalangista cavifrons*, *Phalangista vulpina*, *Didelphys pigmæa*, *Hypsiprymnus*, and a pouch specimen of *Macropus major*. The two species of *Phalangista* and the *Didelphys pigmæa* were adults, the *Didelphys opossum* and the *Perameles* were probably young animals: the *Hypsiprymnus* he described as 'a young,' and the *Macropus major* as 'a mammary foetus.'

In all these animals the thymus gland occupied what might be regarded as the typical mammalian position, being situated in the axilla in front of the trachea and the great vessels; and in some cases extending downwards over the upper part of the pericardium. It did not present, in any of them, a distinct cervical prolongation. Simon's work contained figures showing the form and relations of the thymus in *Didelphys opossum*, *Phalangista vulpina*, and *Macropus major*. In the *Didelphys* he stated that the thymus may be found (fig. 20) to consist of two symmetrical lobes, broader above than below, and having their chief diameter in the vertical direction: they cover the upper third of the pericardium, and reach to the level of the upper edge of the sternum"

¹ Read before the Anatomical Society on the 26th November 1897.

(p. 35). He also wrote, "In a nearly full-grown *Phalangista vulpina* (fig. 21) I discovered a distinct rounded remnant situated on the vessels a little above the heart"; and in the mammary foetus of a kangaroo (*Macropus major*), "I found the gland occupying a position somewhat above the heart, and having a remarkably trifoliate division" (fig. 22).

The conclusions of Simon, "that there is no essential difference as regards this organ between the present and any other family of mammiferous animals," appears to be fully justified by the results of these observations. Although it is more than fifty years since Simon's work appeared, the only additional observation on the thymus in the marsupials that I have found recorded is one by Professor Windle and Mr Parsona¹. In describing the anatomy of *Macropus rufus* they state that, in a pouch specimen of this animal, which measured 13 inches from the snout to the root of the tail, the thymus "occupies its usual position: it consists of two lobes, each of which is about 75 mm. in length" (p. 130).

Last summer, when working in Professor Wiedersheim's laboratory in the Anatomical Institute of the University of Freiburg, I was surprised to discover two large lateral lobes of a thymus gland in a series of sections which I had made through the neck of a pouch specimen of a *Macropus*. These lobes were situated in the ventral part of the neck, immediately beneath the skin and platysma, and superficial to the sterno-mastoids and the depressors of the hyoid bone. They had no connection with any other thymus mass; indeed, there were no other collections of thymus tissue to be seen in the series of transverse sections through the neck. The existence of a thymus in this position was quite new to me, and also to Professor Wiedersheim, who kindly examined my specimens.

As the marsupialia present so many anatomical points distinguishing them from other mammals, it appeared possible that this position of the thymus might be peculiar to and characteristic of them; and further, as the exact development and subsequent history of the thymus are still imperfectly known in many mammals, it seemed advisable to investigate, as far as material

¹ "On the Anatomy of *Macropus rufus*," *Jour. of Anat. and Phys.*, vol. xxxii. part 1, Oct. 1897.

mitted, the anatomy of the thymus in the various marsupial families. The following notes give the results of my work in this direction.

MACROPODÆ.

Pouch specimens.—I have examined eleven pouch specimens belonging to this class. They varied in size from the smallest, with a head length (distance from tip of nose to back of head) of 5 cm., to one with a head length of 6.5 cm. Unfortunately, I am not certain as to the species of the individual specimens, since they were sent me some years ago from New South Wales, without any definite particulars as to the sources from which they were obtained, but I have reason to believe that most of them belong to *Macropus Bennetti*. Of these eleven specimens, four were examined microscopically after being embedded in paraffin and the sections mounted serially; the remaining seven were dissected, and in several of these the structures supposed to be thymus were removed, and this opinion tested by an examination of their minute structure. In two of the fetuses the thoracic viscera had been taken out, but in all of them the neck was in good condition. It is unnecessary to enter into a detailed description of each specimen, as the position and relations of the thymus were essentially the same in all.

The thymus consisted of two completely separate and independent portions, which may be termed, from their respective positions, thoracic and cervical, and in almost every case it was very easy to distinguish two lateral lobes in each region.

The two lateral lobes of the thoracic thymus were placed in the superior mediastinum on the ventral aspect of the trachea and great vessels, and in young mammary fetuses were so small that they were difficult to recognise in an ordinary dissection. Fig. 1 shows a transverse section through the thorax of a pouch specimen of *Macropus*, in which the thoracic thymus is divided. The length of this fetus from snout to root of tail was 2.3 cm., and its head length 7.5 mm. Each lateral lobe formed a rounded body about 3 mm. in diameter.

The thoracic thymus does not appear to grow very fast, or ever to attain a large size. In a specimen whose length from the tip of the nose to the root of the tail was 10 cm., each lateral lobe

was only 3 cm. long; in one 17 cm. it was 6 cm.: and in a still

FIG. 1.—A.

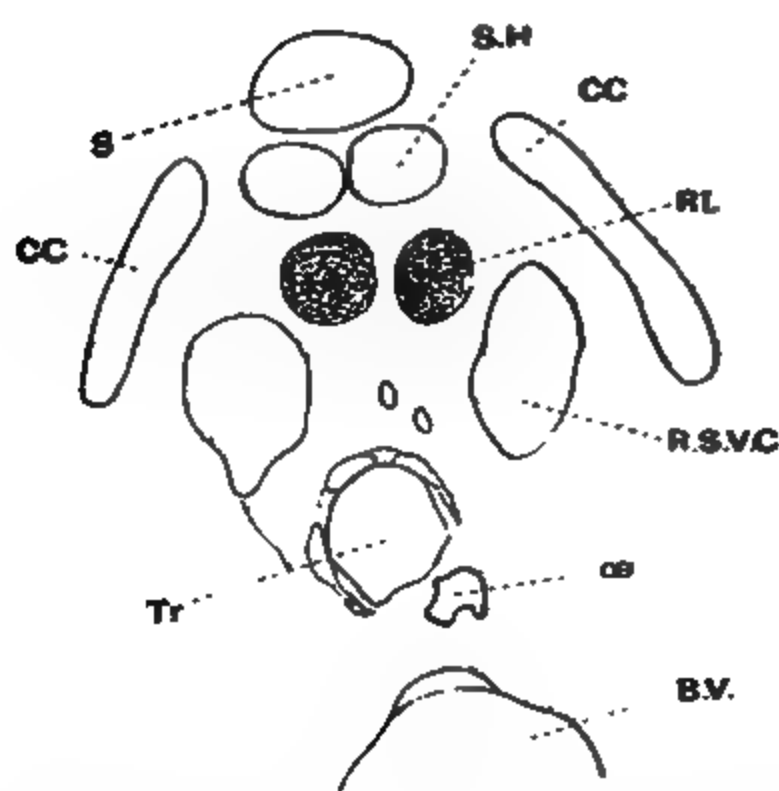


FIG. 1.—B.

FIG. 1.—S, Sternum; B.V, body of vertebra; R.L, right lateral lobe of the thymus; Tr, trachea; OE, oesophagus; R.S.V.C, right superior vena cava; C.C, costal cartilages; S.H, sterno-hyoid muscle.

larger specimen the gland was about 1 cm. long. Windle and

Parsons¹ describe the thoracic thymus as 75 mm. in length in a specimen of *Macropus rufus* which measured 13 inches from the snout to the root of the tail. If this statement were correct, the thymus would be much larger in comparison with the general size of the animal than in any of my specimens, but in answer to my inquiries the authors have kindly looked up their notes and found that 75 mm. is a misprint for 7.5 mm.

The cervical thymus was readily found in all the eleven pouch specimens, although its existence appears to have been hitherto entirely overlooked. As a rule, it is at least twice as large as the thoracic thymus. Its lateral lobes were usually seen to be in close contact near the sternum, where one frequently overlapped the other, but above they diverged somewhat. The relation of the cervical thymus to the integument, and to various structures situated on the ventral aspect of the vertebral column, is shown in fig. 2, which is from a photograph of a transverse section through the neck of a *Macropus* 8 cm. long, head length 2.8 cm. Each lateral lobe is seen to be composed of a number of lobules which show a division into a cortical and a medullary area, the latter being less deeply stained. In the medullary portion of the lobules there are a number of typical Hassall's corpuscles.

In all my specimens except the smallest, the thymus formed a flattened mass, with a ventral or superficial and a dorsal or deep surface, and extended from the submaxillary gland to the sternum. Below, it usually covered a small part of the presternum and clavicles and the adjacent portions of the great pectoral muscles; while its upper end was internal and dorsal to the submaxillary glands. Its outer border was close to the shoulder and, higher up, sometimes touched the parotid gland. In the greater part of its extent it was subcutaneous, only a thin platysma, in addition to the skin and fascia, separating it from the surface. The sterno-mastoid muscles and the depressors of the hyoid bone were close to its deep surface.

Windle and Parsons, in their paper already referred to, give a sketch (see fig. 2, p. 132) of the ventral aspect of the neck of a foetal *Macropus rufus*. In this figure they show the two lateral lobes of a cervical thymus, but they have quite overlooked their

¹ *Op. cit.*, p. 130.

true nature, describing them as extra salivary glands. The structures marked in the same figure 'sublingual' glands are evidently the submaxillary glands.

FIG. 2. A.

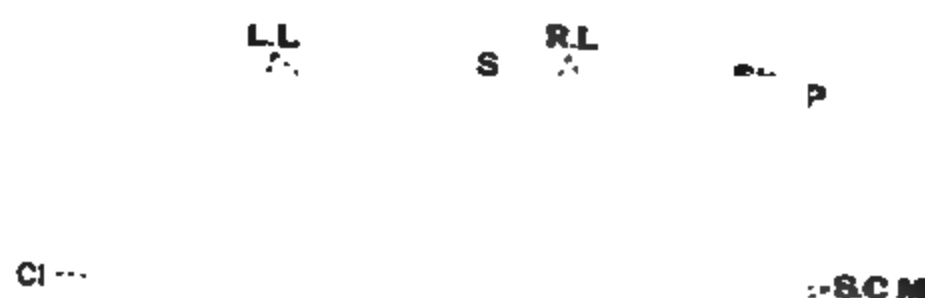


FIG. 2. -B.

FIG. 2.—R.L. and L.L., right and left lateral lobes of the cervical thymus; S., septum of connective tissue between them; S.C.M., sterno-cleido-mastoid muscle; Tr., trachea; O., oesophagus; Cl., clavicle; Sk., skin; P., platysma; V.C., vertebral column.

Adult animals.—Of course, the principal point to be determined by the examination of adult specimens was whether the gland persisted throughout life, or, as in so many mammals, underwent more or less complete atrophy. I have dissected two specimens of Bennett's wallaby; and Professor Melville Paterson,

of University College, Liverpool, has kindly sent me a description and drawing of a dissection of the neck of a *Macropus giganteus*. For one of the specimens of *Macropus Bennetti* I am indebted to Mr F. E. Beddard, F.R.S., and it was particularly useful for my purpose, as its age was known. It was entered in the books of the Zoological Society of London as having been born on the 22nd May 1889, and it died in the gardens on the 29th August 1897, so that it was more than eight years old at the time of its death. The animal was rather fat. In the thorax there was an accumulation of fatty-looking tissue in the usual position for the thymus. Several pieces of this were examined microscopically, but no thymus tissue found. The cervical thymus was embedded in fat, and had undergone partial fatty degeneration, and the limits of its two lobes were indistinct. On microscopic examination, however, typical thymus tissue was found in several places.

The other specimen was sent to me by Dr Berry Hart. It consisted of the thorax; and as the head and neck had been removed by a transverse cut immediately above the sternum, I had no opportunity of examining the cervical thymus. The thoracic viscera were in good condition, and the thymus appeared as two lateral lobes, nearly touching one another in the mesial plane. Each lateral lobe was of a flattened oval form, with the narrow end towards the neck, and measured 1.3 cm. in length and .8 cm. in breadth. They were situated on the ventral aspect of the trachea and great vessels.

Professor Paterson's specimen of *Macropus giganteus* was a large adult, but its exact age was not known. The cervical thymus (see T, fig. 3) consisted of two distinct portions, lying one on either side of the middle line. Each lateral lobe was found under cover of the platysma, invested by a thin sheath of the deep fascia, and resting upon the lower part of the corresponding sterno-cleido-mastoid muscle: it was 3 cm. long and 2 cm. broad, but very thin. It is evident that in this animal the thymus had not grown as fast as the neck generally, unless in this particular *Macropus* the thymus is relatively much smaller than in the pouch specimens I have described. Thus, the distance from the lower border of the cricoid to the episternal notch was 13.5 cm., and the gland was only 3 cm. long, whereas, in my pouch speci-

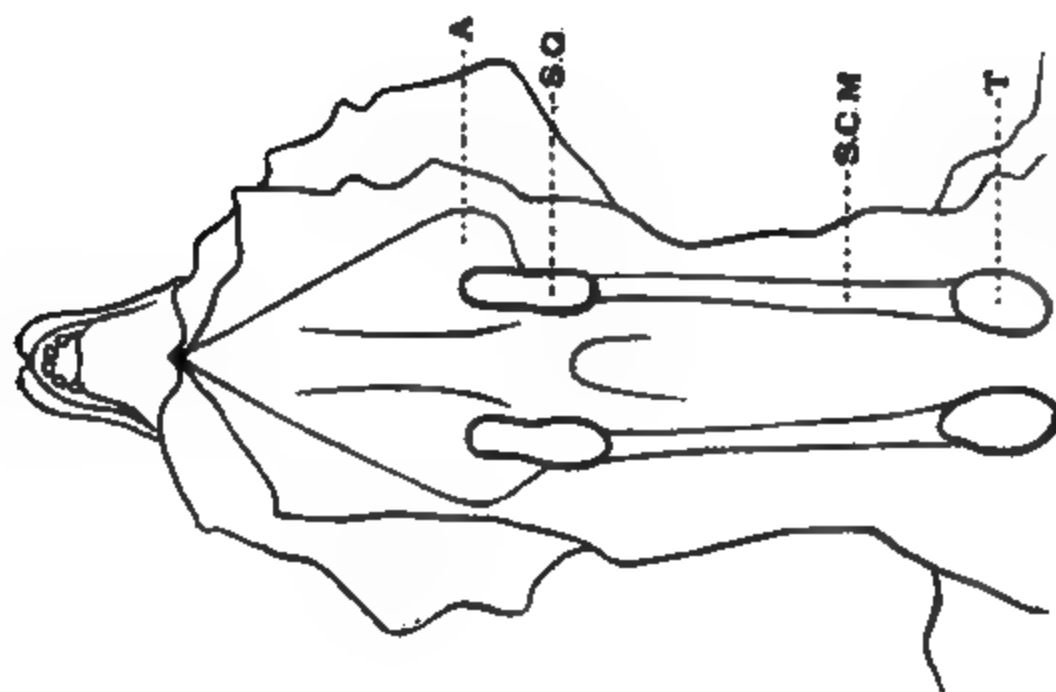


FIG. 3.—B.

FIG. 3.—A

FIG. 3.—View of the ventral aspect of the neck of *Macropus giganteus*, reduced by photography from a drawing by Dr R. C. Dun. A, angle of jaw; S.G., submaxillary gland; T, left lateral lobe of cervical thymus; S.C.M., sternocleidomastoid muscle.

mens, the thymus slightly overlapped the sternum below, and reached to the level of the thyroid cartilage above. Again, in the pouch specimens, the two lateral lobes were in contact with one another, and here the distance between them was 2 cm.

PHALANGISTIDÆ.

In this family I have made microscopic sections of two young specimens, for one of which I have to thank Professor Wiedersheim. Both were probably vulpine phalangers. The smallest of these specimens measured from the front of the head to the root of the tail 20 mm. and its head length was 7 mm.; the corresponding dimensions of the other fœtus being 30 mm. and 13 mm. It is unnecessary to enter into any description of the thymus in these specimens, as it was practically identical with that found in the young pouch kangaroos.

I have dissected two adult vulpine phalangers (*Trichosurus vulpecula*). I am indebted to Professor Charles Stewart, F.R.S.,

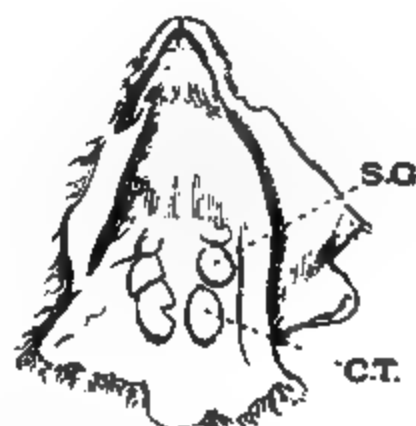


FIG. 4.—A.

FIG. 4.—B.

FIG. 4.—Ventral aspect of the neck of an adult vulpine phalanger (*Trichosurus vulpecula*). Skin, platysma, and part of parotid glands reflected. C.T., left lobe of cervical thymus; S.G., left submaxillary gland. A piece had been cut out of the right lobe for microscopic examination.

for the opportunity of examining one of these; the other was from my own collection. On dissecting the front of the neck in these animals the parotid gland was found to reach down as far as the shoulder and clavicle, and to extend forwards, as a thin flat mass, to the median plane, where in several places the glands

of opposite sides appeared to be continuous. On reflecting these glands and a layer of deep fascia, the cervical thymus was found to consist of two distinct lateral lobes, which reached within half an inch of the sternum, and were overlapped above by the submaxillary glands. In my specimen each lobe formed a somewhat oval flattened mass 20 mm. long and 12 mm. broad, and its deep surface was in relation with the depressor muscles of the hyoid and the sterno-cleido-mastoid muscle. The two lateral lobes were about 4 mm. apart.

In the thorax there was a thymus, the two lateral portions of which were in contact, the left covering slightly the adjacent portion of the right lobe. It was more than half the size of the cervical thymus.

PHASCOLOMYIDÆ.

I have not succeeded in obtaining any pouch specimens of the wombat, but have dissected the thymus in three adults. Two of these I examined with Professor A. H. Young in The Owens College, Manchester, and the third was sent me, immediately after its death, from the Dublin Zoological Gardens, by Professor D. J. Cunningham. In all these animals the cervical thymus had essentially the same position and relations as in the phalangiers and kangaroos. The skin, a well-developed platysma, and a distinct sheath of deep fascia formed their superficial covering. The inner borders of the two lateral lobes were parallel with the median plane, and separated from one another by a distance of nearly an inch. Each lateral lobe resembled the corresponding body in the vulpine phalanger, and differed from that of the *Macropus giganteus* dissected by Professor Paterson, in being in close relation with the submaxillary gland. Each lobe was about 3 mm. thick; their lengths in the three specimens were respectively 45 mm., 38 mm., and 32 mm., and breadths 37 mm., 32 mm., and 25 mm.

In the specimen sent me by Professor Cunningham, I opened the thorax and found some loose fat in front of the large vessels and the upper part of the pericardium. In this fat, on the right side, there was an irregularly shaped thymic lobule about 18 mm. long, but I could not find anything resembling the thymus on the left side.

DIDELPHYIDÆ.

My material belonging to this family consisted of four specimens of *Didelphys virginiana*.

1. A young pouch specimen presented to me by Professor Wiedersheim. Its length from the front of the head to root of the tail was 25 mm. and its head length 12 mm.

2. A hairy pouch specimen. Its total length, excluding tail, was 9 cm., and its head length 4 cm.

3 and 4. Two adults, for the younger of which I have to thank Dr Berry Hart.

In No. 1 the thorax and the head and neck were embedded in paraffin and all the sections mounted serially; the other specimens were dissected. In none of them could I find the slightest trace of a cervical thymus.

In the smaller pouch specimen the thoracic thymus was well developed, being relatively much larger than in any of the *Macro-podidæ* examined. It extends from the level of the top of the sternum caudad, so as to cover the upper part of the pericardium and auricles. At its two extremities it showed a division into lateral halves, but the intermediate portions had blended to form a lobulated mass in the transverse sections, of which there were no traces of a median connective tissue septum.

In each of the remaining three specimens the thoracic thymus was easily found, but it was of small size, and only partially divided into two lateral lobes.

I regret that I have not been able to examine specimens belonging to the two remaining families of the marsupialia, viz., the *Peramelidæ* and the *Dasyuridæ*. It will be noticed that it has been shown that in the three families forming the diprotodont division of the marsupialia, the thymus consists of two parts—a thoracic and a cervical, the latter being the larger, and forming two lateral lobes, which occupy a superficial position in the ventral part of the neck, and are entirely distinct from the thoracic thymus. In the polyprotodont group I have only examined one family, viz., the *Didelphyidæ*, and in this the cervical thymus is entirely absent even in a young pouch specimen. It will be of interest to see if the *Peramelidæ* and the

Dasyuridae agree with the *Didelphyidae* in the arrangement of their thymus, or show affinities in this respect with the diprotodont families. The *Dasyuridae* are generally regarded as the most primitive of the marsupials, and the family includes the most typical carnivores. Should the cervical thymus be found absent in them, it cannot be regarded as a character of the primitive marsupial type, but one that has been acquired in the more specialised diprotodonts, possibly in association with their vegetable diet and the call for a larger amount of thymic tissue.

In this connection it is of interest to note that in the carnivora of eutherian mammals the thymus is generally small, usually confined entirely to the thorax, and atrophies early. In the ungulates, on the other hand, it is often of large size, is situated both in the thorax and the neck, and frequently persists in the adult. This cervical portion differs, however, in several important respects, in its position and relations, from the cervical thymus of marsupials. Thus, in the calf it begins in front as two lateral portions, which lie in close relation with the corresponding submaxillary glands. These two parts pass backwards and inwards to reach the ventral surface of the trachea, where they unite to form a thick mass situated on the deep aspect of the depressor muscles of the hyoid bone. From this a thin process goes backwards into the thorax, and becomes continuous with another enlargement which is in relation with the pericardium. It thus differs from the marsupial organ in lying on a deeper plane, in becoming continuous with the thoracic thymus, and in showing a decided tendency for the two lateral parts to fuse.

It does not fall within the scope of this paper to refer to the large mass of literature dealing with the development of the thymus in the various classes of the Vertebrata, but there are a few points of interest bearing upon its condition in the marsupialia which may be briefly noticed. The thymus is developmentally a bilateral organ, and each half possesses, as a rule, a multiple origin. Thus, in the skate it arises, according to Dohrn and others, by epithelial diverticula from all the five functional gill-clefts; and although the number of these diverticula tends to diminish with the reduction in number and early disappearance of these clefts, yet even in mammals it probably takes origin from the 4th as well as the 3rd pair of clefts. The complete separa-

tion of the thoracic and cervicæal portions of the thymus, even in young pouch marsupials, suggests the probability that they have a different origin,—one arising from one cleft and the other from another. Further, the superficial position of the cervical thymus may be associated with the origin from the epiblastic rather than the hypoblastic portion of the clefts. These questions, however, must remain matters of speculation until some one with opportunities for obtaining suitable material investigates the very early stages in the development of the thymus in the marsupialia.

It is probable that the thymus is represented in many mammals, especially during early foetal life, by several separate and independent bodies. Kohn¹ has shown that in various mammals there are two small masses of 'adenoid' tissue, closely united with each lateral lobe of the thyroid. These masses have the structure of ordinary thymus tissue, including the epithelial nests, or the so-called Hassall's corpuscles. More recently, I² have described the existence in a foetal sloth of a relatively large thymus lobule situated on the dorsal aspect of each lateral lobe of the thyroid, but not closely connected with the thyroid.

None of my marsupial specimens were sufficiently young to show whether or not their thymus is developed, like ordinary mammals, as an organ composed of epithelium arranged to form hollow tubes. In some of them, however, it had not acquired its typical structure. Thus, in my youngest *Macropus*, which had a head length of 7.5 mm., the thymus contained no Hassall's corpuscles, and the majority of the cells appeared to me to be of an epithelial type, and in a few places they formed distinct tubes. In the young pouch specimen of *Didelphys virginiana*, in which the head was 12 mm. long, the majority of the cells were lymphoid in appearance, but there were groups of epithelial-like cells, and in various sections epithelial nests in process of formation could easily be recognised.

In a *Macropus*, with a head length of 2.8 cm., whose thymus is shown under a low power in fig. 2, the microscopic appearances of the gland were those of a fully developed thymus.

¹ "Studien über die Schilddrüse," *Archiv f. mikros. Anat.*, Bd. xlv., 1895.

² "Ueber Thyreoidea, Glandulæ parathyroideæ und Thymus beim dreizehigen Faulthier (*Aï, Bradypus tridactylus*)," *Arch. für Anatomie*, Supplementband W. H. gewidmet., 1897.

As is well known, there are some histologists who hold that the lymphoid cells of the thymus are derived by direct descent from its primitive epithelium, while others describe a leucocyte invasion of this epithelium, these epithelial cells in great part disappearing, but some of them remaining in Hassall's corpuscles.

The object of my investigation was mainly to determine the topographical anatomy of the thymus, and my material had not been fixed sufficiently well, stained with the requisite care, or cut thin enough to entitle me to express a decided opinion on this disputed point. I am disposed, however, to support the view of a leucocyte invasion as giving rise to the lymphoid cells, rather than to regard these as originally epithelial.

This work was commenced last summer in the Anatomical Institute of the University of Freiburg; and I desire to thank Professor Wiedersheim for his great kindness in affording me every facility for my investigations, presenting me with several valuable specimens, and allowing me free access to his private library.

Miss Clara Patterson has mounted and photographed a considerable number of the sections. Mr Andrew, L.D.S., took the micro-photograph shown in fig. 1, and Mr H. M. M'Crea, one of my students, photographed the dissection represented in fig. 4.

27th November 1897.—Since writing this paper, I have had the opportunity, through the kindness of Professor C. Stewart, of dissecting the neck of an adult dasyure (*D. cancrivora*), and could find no traces of a superficial cervical thymus. This specimen thus supports the view, suggested above as probable, that this portion of the thymus is absent in the polyprotodont Marsupials.

CONCERNING THE PARATHYROID GLANDS : A
CRITICAL, ANATOMICAL, AND EXPERIMENTAL
STUDY.¹ By D. A. WELSH, M.A., M.D., *Assistant to the
Professor of Pathology in the University of Edinburgh ;
Pathologist to the Royal Hospital for Sick Children,
Edinburgh.*

INTRODUCTION.

THE first part of this paper will consist of a critical historical digest of the literature concerning the parathyroid glands, in so far at least as it relates to anatomical and experimental work. A number of interesting and valuable references to their mode of development and embryological structure have been omitted, as it is intended that these should be included in a subsequent publication. With this exception, however, an endeavour has been made to give a more complete account of the literature down to the beginning of 1897 than has hitherto been published.

The second part will comprise an original investigation into the structure and arrangement of the parathyroid glands in man, with a reference to these organs in some other mammalia. It is remarkable that no contribution of any importance has been made to the anatomy of the human parathyroids since their original discovery in 1880. Even the most recent English text-books in anatomy practically ignore the structure of these glands in man, and describe chiefly those of the cat.

In the third part, all that can be given is a brief synopsis of a preliminary experimental study of the parathyroid glands of the cat. A more detailed description will be found in the *Journal of Pathology and Bacteriology* for 1898.

¹ This paper formed the greater part of a thesis which was presented in May 1897 for the degree of Doctor of Medicine of the University of Edinburgh, and for which a gold medal was awarded.

PART I.

A CRITICAL HISTORICAL DIGEST OF THE LITERATURE CONCERNING
THE PARATHYROID GLANDS.I. *Anatomical Section.*

The presence of isolated glandular bodies in the more or less immediate neighbourhood of the thyroid gland has long been known, and their not infrequent occurrence has been noted by numerous authors. But up to the year 1880, and even for some time later, all such bodies were described as accessory thyroid glands, as masses of adenoid tissue, as carotid glands, or simply as obscure structures.

It is essential to observe at the outset that, although the parathyroid glands are, in a sense which will appear later, accessory to the thyroid, yet the terms 'accessory thyroid glands' and 'parathyroid glands' have, or ought to have, widely different connotations. In the former term are included those nodules of thyroid tissue which, having at some period of development become detached from the main body of the gland, still appear to be both structurally similar and functionally equivalent to it. They are further characterised by the inconstancy of their occurrence and by the uncertainty of their position, having been found at all levels, from the supra-hyoid region to the region of the aortic arch. The latter term is applied to independent structures, which are remarkably constant both in their number and in their position, which at no stage in their development correspond in structure to the thyroid gland of the same stage, and which appear to have a very special function.

A considerable number of writers have given their attention to the mode of origin and ultimate localisation of accessory thyroid glands in man and in other animals, but in none of the earlier papers to which I have had access have I been able to find any explicit reference to the parathyroid glands, for either a histological record is wanting or the structure is obviously dissimilar.

Thus *Virchow* (41) in 1863 stated that he had found with

extraordinary frequency, on the posterior surface of the lateral thyroid lobes, small rounded bodies about the size of a pea, which were united to the thyroid by loose connective tissue, and which appeared to be either small lymph glands, or detached portions of thyroid tissue. It is remarkable that so keen an observer as he should have failed to recognise another characteristic structure which occurs with great uniformity in the same position; for, in all likelihood, many of the bodies which he thus summarily dismissed were really parathyroid glands, although both accessory thyroid glands and masses of adenoid tissue—chiefly thymus residues—occur in the same position.

Both before and after this date accessory thyroid glands were described by Gruber, Verneuil, Callender, Bruch, Porta, Simon, Paget, Kroenlein, Poland, Kadyi, Zuckerkandl, Madelung, Wölfler, Wagner, Fuhr, Carle, Wolf, Semon, Piana, Ewald, Autokratow, Gibson, and many others, all of whom, however, appear to have entirely overlooked the parathyroid glands.

In 1880, as has already been indicated, the parathyroid glands were definitely discovered by *Sandström* (37), who found that in man, and in several other animals of the mammalian series, there were constantly present in or near the thyroid small epithelial glandular organs, which he designated 'glandulæ parathyroideæ.'

In man, he described two parathyroid glands on each side, one above and one below the inferior thyroid artery, on the posterior surface of the lateral thyroid lobe, and near its lower margin. Although in close proximity, they were never actually continuous with the thyroid structure, but were invariably separated from it by a zone of connective tissue. The minute anatomy of these bodies showed great variety, but there were three main types to which their structure tended to conform: (1) a continuous mass of epithelial cells, penetrated by a somewhat dense capillary network; (2) a continuous cellular reticulum, the meshes of which were occupied by blood-vessels and connective tissue; (3) numerous small follicles, in a connective-tissue stroma. In this last type there were frequently present small masses of a substance whose micro-chemical reactions resembled those of thyroidal colloid.

In the course of my own work on the anatomy of the human

parathyroid, I have been able to corroborate most of Sandström's results. I have, unfortunately, not been able to procure his original paper, which is in Swedish, but some of the contemporary German reviews, especially that in Schmidt's *Jahrbuch*, are somewhat fully detailed, and I cannot too strongly emphasise the admirable precision and accuracy which characterise this earliest record of these glands in man.

The other mammalia examined by him included the dog, cat, ox, horse, and rabbit, in all of which he found similar organs, but only one on each side,—in fact, he discovered the external parathyroid in these animals.

Although his work was purely anatomical, he hazarded a conjecture as to their physiological significance. He stated that all the variations in their structure corresponded to different stages of thyroid development; and he therefore considered that they were essentially embryonic residues of the thyroid, destined to form fresh thyroid tissue when required. He does not appear to have made any examination of the embryonic parathyroid, otherwise he would probably have observed its early differentiation from the thyroid.

The merit of this discovery is undoubtedly shared by an English observer, who, however, did not so fully realise its significance; for there can be no doubt that the 'undeveloped portions' of the thyroid gland described by *Baber* (1) correspond to the 'glandulæ parathyroideæ' of Sandström. These 'undeveloped portions' were especially found in the thyroid of the dog, but similar structures were occasionally present in those of the kitten, sheep, seal, rook, and pigeon. It is interesting to note that Baber, though he failed to recognise their constant occurrence in the animals examined by him, yet independently formulated the same conclusion as Sandström regarding their embryonic residual nature, and later potential development. Both authors thus anticipated the theory advanced more than ten years later by Gley in support of his experimental results.

Although Sandström's work was noticed in some detail in contemporary journals, yet his discovery was almost entirely neglected. *Krause* (22) appears to be almost the only author who took advantage of it, for he makes mention of the parathyroids both in his treatise on Human Anatomy, published in 1881, and in the second edition of his Anatomy of the Rabbit, published in 1884.

In the Brown Lectures on Pathology delivered in 1885, *Horsley* (19) stated that he had specially investigated the embryonic tissue of the thyroid previously described by Baber. In some animals a large quantity of this tissue could be found in a single mass beneath the thyroid capsule, but separately and distinctly encapsuled. He maintained that although the tissue was regarded as embryonic, still it had not been demonstrated that it ever developed into acini; but that, on the contrary, the result of researches into this matter had hitherto rather tended to oppose the likelihood of such a supposition being true. The publication of this description by Horsley of what must now be regarded as the parathyroid gland seems to have been quite overlooked by subsequent authors.

In 1888 *Rogowitch* (33) very cursorily described the occurrence of 'restes embryonnaires' in the thyroid glands of young and of adult animals, and he illustrated them by reference to what is obviously the internal parathyroid of the dog. These bodies, he says, are sharply defined from the rest of the thyroid tissue, and in their structure correspond, according to the age of the animal, to different phases in the development of the thyroid,—a statement which is not strictly accurate. He goes on to say that their transformation into true colloid follicles occurs a long time after birth, when other methods of growth of the thyroid have become exhausted,—an exceedingly doubtful hypothesis.

No further reference was made until the publication of *Gley's* (9) preliminary note in 1891; but as his work is chiefly experimental, further consideration of it is deferred.

In the Bradshaw Lecture on some Diseases of the Thyroid Gland, delivered in 1893, *Greenfield* (10) refers to undeveloped glandular spaces, often in clustered masses, in the normal structure of the thyroid. In all probability, however, his description has reference to integral portions of thyroid tissue, and not to parathyroid tissue, properly so called.

Cristiani (4) in 1893 followed up Gley's researches by investigating the parathyroid of the lesser rodents, including the rat, the common mouse, and the field mouse. In all the animals examined he observed only one on each side corresponding to the external parathyroid of the rabbit. In the rat, the relation of the parathyroid to the thyroid was found to be most intimate, the former being completely inclosed in the outer surface of the main gland, though never continuous with it. In the common mouse the connection was less intimate, the parathyroid projecting above the surface of the thyroid, and often partially detached from it. In the field mouse the separation was still more marked, so that one parathyroid was frequently completely severed from the thyroid. In structure they showed no essential difference from those of the rabbit, and were again regarded as portions of embryonic thyroid tissue.

In 1894 masses of embryonic tissue in the thyroid gland of the dog were described by *Hürthle* (18) and by *Zielinska* (45). Their description corresponds sometimes to the external, sometimes to the internal parathyroid of that animal. Both authors consider that

they represent stores of reserve material, and that, when necessity arises, fresh thyroid follicles may be developed from them.

In 1895 *Kohn* (24) published an elaborate study of the parathyroid glands in the cat and in other animals, and was the first to make any distinct anatomical advance on *Sandström's* earlier work. Perhaps his most important contribution lay in the discovery that there were constantly present two parathyroid glands on each side in the cat, dog, and rabbit. Since these were the animals chiefly employed for experimental research, and since only one on each side had been recognised by previous observers, the significance of his work is at once obvious.

He was also amongst the first to dispute the statement, hitherto almost universally accepted, though contradicted in 1894 by *Prenant* (32), that the parathyroid glands were simply embryonic residues of thyroid tissue. He maintained that, on the contrary, they were perfectly independent structures, both morphologically and functionally distinct from the thyroid. For this reason he took exception to the term 'parathyroid' as implying a genetic relation to the thyroid, which had still to be proved, and preferred to use the indifferent term 'epithelial corpuscle of the thyroid,' distinguishing them further as 'external' and 'internal' according to their relation to the lateral thyroid lobe.

The external parathyroid gland ('the external epithelial corpuscle of the thyroid') was invariably present in all the animals examined by him, including, in addition to those already mentioned, the mouse, rat, guinea-pig, and one case in man. Its position, relatively to the thyroid, showed considerable variation, but there was never, with the exception of a very small area in two of the cats examined, any continuity of tissue, the two structures being everywhere separated by an uninterrupted zone of vascular connective tissue. Histologically, three types were found, according to which the arrangement of the epithelial cells might be classified: (1) a dense continuous mass of cells, with no indication of a network; (2) a continuous reticulum of cellular trabeculae, sometimes slender, sometimes broader; (3) definite lobule formation, each lobule consisting of delicate cellular trabeculae which anastomosed. *Kohn* does not appear to have met a histological type which is very common in the human parathyroid, and in which the epithelium forms distinct acini, with a central lumen, frequently occupied by colloid material. In fact, he expressly denied the occurrence of any colloidal substance in the parathyroids examined by him.

I have, so far, not found any colloid in the parathyroid of the cat, but it is relatively abundant in that of man.

The internal parathyroid ('the internal epithelial corpuscle of the thyroid') was not found in all the animals investigated, but only in the rabbit, dog, and very typically in the cat. It differs in two important particulars from the external parathyroid.

(1) Not only is it situated on the internal or tracheal surface of the lateral lobe, but it is, as a rule, completely covered by the thyroid tissue, so that it is not visible from the surface, and is therefore difficult to find except in serial sections.

(2) It regularly enters into extensive combination with the tissue of the thyroid, and with that of the corresponding thymus lobule, whereas a union of the external parathyroid is quite exceptional.

In 1896 *Kohn* (25) published a second paper on the anatomy of the parathyroids, with special reference to those of the rabbit. As a result, he was still further confirmed in his theory of the constant occurrence of the parathyroid, both external and internal. He discovered several fresh facts of interest, the most important of which perhaps is, that in very young rabbits the external parathyroid is usually found at a higher level than in full-grown animals. It may indeed be met as high as the oral pole of the thyroid; but, as age advances, it appears to change its position, so that it comes to lie some distance below the thyroid.

Shortly after the appearance of Kohn's earlier monograph, *Schaper* (39) published an account of certain structures which he had found in the region of the carotid bifurcation, and which he identified with the parathyroid glands. He examined these regions in calves, in sheep, and in five cases in man; and his results are for the most part at variance with those of Sandström and of Kohn. It is not possible to discuss all his numerous conclusions, founded as they are on insufficient data: two points only can be noticed.

(1) He alleged that the parathyroids are found more certainly near the carotid bifurcation than near the thyroid, and that in any case their number is indeterminate. Positive evidence, however, must always outweigh negative, and the explanation of his results lies probably in the fact that he examined too few cases, and that many of those he did examine were very young. In very young animals, as Kohn has demonstrated, the parathyroids are situated at a somewhat higher level than in adults.

(2) He maintained that the parathyroids were really embryonic thyroid residues, and that he had observed their development to actively functional thyroid tissue. Such a conclusion is quite unwarranted either by the embryonic or by the adult structure of the parathyroid.

In 1896 *Schmid* (40), in the course of his studies on the thyroid, refers to the parathyroids as "the external and the internal embryonic residue of the thyroid." He contrasted the continuous cellular network found in the parathyroid of the cat with the arrangement which he met in that of the dog, in which he found clusters of cells, disposed, as a rule, concentrically round a small lumen or a globule of colloid

matter. Hence he concluded that the parathyroid of the dog represented a stage in the development of the embryonic tissue higher than that of the cat—an inference for which it is not easy to see the justification.

Nicolas (30) is quoted by Schaper as having observed in the Cheiroptera two nodules on each side of the thyroid. Presumably these were the parathyroids, but I have not been able to consult the original, and the reference is far from clear.

L. R. Müller (29), in 1896, examined the thyroid and the adjacent glands in 22 cases in man, from birth to old age, and also in the dog and cat. As regards the parathyroids, his results in the main agree with those of Kohn; but he stated that he was not in a position to estimate the frequency of their occurrence in man, as he had found they were easily overlooked. He noted the occurrence of colloid follicles in the human parathyroid—a common condition; and also in that of the cat—a condition which I have never seen.

II. *Experimental Section.*

It has long been known that different species of animals do not equally resent extirpation of the thyroid, and that, even within the same species, striking and unaccountable differences occur. It is possible, however, roughly to classify the various kinds of animals in the order of their susceptibility, and this was done by *Horsley* (20), to whose writings I am indebted for the outlines of the following scheme:—

Class 1.—Animals which show practically no symptoms after thyroidectomy:—(a) Aves, *e.g.*, chickens and pigeons; (b) Rodentia, *e.g.*, rabbits.

Class 2.—Animals which show a slow and uncertain cachexia, which may terminate fatally after a long interval of time:—Ungulata, *e.g.*, sheep, goat, donkey, pig.

Class 3.—Animals which show a well-marked chronic cachexia, with an almost invariable fatal termination:—Anthropoidea, *e.g.*, man and monkey.

Class 4.—Animals which, as a rule, show intensely acute symptoms, with a rapidly fatal result:—Carnivora, *e.g.*, dog, cat, and fox.

It was therefore thought that the marked variations in the susceptibility of different animals corresponded to differences in their metabolism. Flesh-eating animals were supposed to suffer most acutely, while those which were restricted to a vegetable diet suffered least, omnivora occupying an intermediate position.

This hypothesis received further support from *Breisacher* (2), whose experiments showed that dogs fed on fresh meat suffered more acutely from thyroidectomy than those fed on milk or boiled meat. From this he inferred that the extractives of raw flesh can, by some undetermined action on tissue metabolism, intensify the symptoms that follow removal of the thyroid.

In a preliminary note communicated in 1891, and in a series of papers published in 1892 and 1893, *Gley* (9, 12, 13) offered an entirely different explanation. He contended that the difference was more apparent than real, and that it arose from an essential difference in the operation performed. He pointed out that in the rabbit the (external) parathyroid was usually quite separate from the thyroid, and situated about half a centimetre below it; whereas in the dog the corresponding organ was closely incorporated with the lateral thyroid lobe. In all probability, therefore, thyroidectomy in the rabbit had previously involved removal of the thyroid alone, but thyroidectomy in the dog had implied removal of the thyroid and parathyroids together. It is to be understood that the internal parathyroid gland was then unknown, and that throughout the whole course of his earlier experiments *Gley* remained in complete ignorance of its existence.

(1) He accordingly investigated the effect of removing both thyroid and parathyroid in the rabbit, an operation which he terms "thyroïdectomie complète." His results were most striking. Out of 16 rabbits thus operated on, only 2 survived beyond a week, both being accidentally killed. The remaining 14 rabbits showed a rapid onset of symptoms, and a rapidly fatal result. In the great majority of cases the symptoms began within 24 hours after the operation, and led to death a few hours later; on dogs, on the other hand, it was rare to meet any symptoms before the end of the second day, and rare to have death until several days later. The symptoms themselves presented a remarkable analogy to those previously observed in the dog, and a very marked contrast to those previously observed in the rabbit. By the end of 1893 *Gley* had performed "thyroïdectomie complète" on 55 rabbits, of which only 12 had survived. A possible explanation of this discrepancy may be found in the fact that portions of the internal parathyroid may sometimes have been left behind, though usually completely removed, owing to its

close connection with the thyroid. From these experiments he concluded that removal of the thyroid and parathyroids together was practically as fatal in the rabbit as in the dog.

(2) Gley next showed that it was possible, even in the dog, to remove the thyroid and leave the two (external) parathyroids intact. He gives a description of this somewhat delicate operation, which he performed in 10 cases. Of these only 2 died (one had an empyema, in the other only one parathyroid had been left), and the remainder showed no symptoms for many days. Subsequent removal of the parathyroids in the same dogs led to the usual rapidly fatal termination, with all the symptoms characteristic of former operations for thyroidectomy. Removal of the thyroid alone he therefore considered to be as innocuous in the dog as in the rabbit. In reality Gley had removed not the thyroid alone, but probably also the internal parathyroids; and what he showed was, that the external parathyroids alone could, in the dog and in the rabbit alike, avert a fatal issue.

(3) Extirpation of the parathyroids alone (*i.e.*, of the external parathyroids) was productive of no result either in the dog or in the rabbit.

(4) Removal of the thyroid (and internal parathyroids) in the rabbit led, as was anticipated, to no symptoms; but if, a month later, the (external) parathyroids were also removed, then the animals died, with acute symptoms similar to those resulting from simultaneous removal of both thyroid and parathyroid glands, while the parathyroids were found to have undergone a compensatory hypertrophy, and a partial development to mature tissue.

The publication of these experimental results gave an impetus to further research on this subject; and several investigators contradicted, while others supported Gley's conclusions. Much of the work of this period, however, is little better than a groping in the dark, owing to the lack of anatomical precision.

One of the first to challenge Gley's results was *Moussu* (27), who in 1892 and 1893 claimed to have removed the thyroids and the parathyroids in 19 rabbits, of which only 4 succumbed. As I shall again have occasion to point out, a mere statement that the parathyroid has been excised is not a sufficient guarantee that it has actually been removed, unless a histological examination is in every case made. *Moussu* also operated on the horse, donkey, ram, and goat, but he failed to find any parathyroid glands in these animals. It does not of course follow that the glands were really absent.

Hofmeister (17) removed the thyroid in young rabbits, and observed that there occurred a profound interference with development, more especially with that of the osseous system. He concluded that the parathyroid glands, which he presumed to have been left behind, were not sufficient, at least in young rabbits, completely to compensate for the loss of the thyroid, a conclusion which Gley accepts. It is not so certain, however, that the parathyroids were always left behind in these cases, for in young rabbits the external parathyroids may occupy a position near the cephalic pole of the thyroid, and may thus be readily removed along with the thyroid.

Cristiani (4), in 1893, supplemented Gley's results to some extent by showing that complete thyroidectomy was fatal in the rat, an animal which had previously been found insusceptible by Schiff and Philipeaux.

In 1895 *Gley* (15), in association with Nicolas, made a more careful study of the changes in the parathyroids (external) after removal of the thyroid. They investigated the rabbit alone, and found (1) that after 15 days there was a slight but distinct enlargement of the parathyroids; (2) that this was accompanied by an alteration of the staining reactions of the epithelial cells, and in two cases by the appearance of mitotic figures in them; (3) that even after longer intervals of 3, 4, and 12 months there was no evidence of transformation to thyroid structure.

From 1894 onwards the earlier results obtained by Gley were essentially confirmed by Verstraeten and Vanderlinden in Belgium, by Cadéac and Guinard, and by Rouxeau in France, by Paladino and by Capobianco in Italy, and by Edmunds in England. It is not, however, necessary to give all the details of the work of these various authors, as much of it is merely confirmatory of previous experiment, and all of it was done before Kohn's anatomical researches were known. A brief outline is all that will be given (*cf.* Gley (11)).

Verstraeten and *Vanderlinden* (44) found that removal of the thyroid and parathyroids together was almost invariably fatal in the rabbit, but that the symptoms were not usually so acute as those originally described by Gley. They also found that, after removal of the thyroid, the (external) parathyroids left *in situ* showed at first vascular engorgement, and later considerable increase in size. Even the supporting connective tissue was increased, while the columns of epithelial cells became enlarged, not by a proliferation of their elements, but by a "true hypertrophy" of the individual cells. It is somewhat doubtful how far these authors have correctly interpreted histological changes, the conditions they describe being more consistent with a process of inflammation than with one of hypertrophy.

Cadéac and *Guinard* (5) merely state that, in opposition to Moussu and in accordance with Gley, they have found that "thyroïdectomie complète" is as fatal to rabbits as it is to dogs.

Paladino (31) and *Capobianco* (6) also state that in their experience rabbits and dogs equally succumb to loss of the thyroid and parathyroids together. The resulting symptoms, however, differed in so far as none of the rabbits—30 in all—ever had a convulsive attack, —only fibrillary contractions and slight localised spasms.

In 1895 *Edmund* (8) communicated to the Physiological Society the results of his valuable experiments on rabbits and on dogs, and is, so far as I am aware, the only observer in this country who has published any experimental work on the parathyroid glands.

He repeated Gley's experiments on rabbits, and found (1) that if both the thyroid and the parathyroid glands were removed the animals died; (2) that when the thyroid alone was excised, the (external) parathyroids being left, many of the animals also died, sometimes in a condition resembling myxœdema in man; (3) that if the (external) parathyroids alone were extirpated, the animals as a rule lived, and did not undergo any obvious change, at least not for a long time.

The result of his experiments on the dog was to show "that if the whole of one lobe of the thyroid, including its (external) parathyroid, and also the greater part—two-thirds or more—of the other lobe be removed, the animal will live or die according as the (external) parathyroid is or is not left."

The term 'parathyroid' refers, as in all previous experiments, solely to the external gland, the corresponding internal organ being at that time unknown, and probably always removed or retained according as the thyroid was removed or retained.

Rouxau (35) published in 1895 the first of an extensive series of experiments on the rabbit. Further results followed in 1896, and finally the complete series of 103 experiments appeared early in 1897. (1) In 46 rabbits he removed the thyroid and parathyroids at one operation, and found that four-fifths presented severe and characteristic nervous symptoms; (2) in 57 rabbits he removed the thyroid, leaving the (external) parathyroids, with the result that only 1 showed characteristic symptoms, though 12 others died, at varying intervals, of broncho-pneumonia; (3) in 13 rabbits he removed the thyroid with no result, and some time later the (external) parathyroids, the second operation being in every case followed by acute symptoms, culminating in death.

In 1896 there appeared a paper by *Blumreich* and *Jacoby* (3), who assailed Gley's conclusions in almost every particular. They maintained (1) that in the rabbit there was no difference between those animals from which the thyroid alone had been removed and those which had lost both the thyroid and the parathyroids (*Nebenschilddrüsen*); (2) that the prognosis after thyroidectomy was not in the least improved by leaving two parathyroids in place of one; (3) that the parathyroids left after thyroidectomy were never found to have undergone the slightest hypertrophy. It is difficult to reconcile their results with those of previous investigators. They are directly opposed to the consensus of opinion reached by equally skilled observers.

The first to avail themselves of the anatomical data supplied by Kohn were *Vassale* and *Generali*, a short account of whose work appeared in 1896, and they were followed in 1897 by *Gley*, *Rouxau*, and *Moussu*.

Vassale and *Generali* (42) were the first to remove all the four parathyroid glands, leaving the thyroid *in situ*. This operation was performed on 10 cats and 9 dogs. Of the cats, 9 had succumbed by the tenth day, and one had been living for a month at the time of writing. They all suffered from characteristic morbid symptoms, fibrillary tremors, muscular twitchings, depression, rigid and staggering gait, anorexia, emaciation, and lowering of the body temperature. Of the 9 dogs, all died within eight days, and on an average between the third and fourth day: symptoms began in the second and third day, and were analogous to those which resulted from ordinary thyroidectomy in the dog or in the cat, *i.e.*, from simultaneous removal of the thyroid and parathyroids. As a rule, however, convulsive attacks were wanting or were slightly marked, and only at the end; on the other hand, there predominated phenomena of diminished excitability of the nervous system, and forms of paralysis which rapidly killed the animal.

In a subsequent paper they record a series of operations on the dog, designed to test the functional significance of the parathyroids relatively to each other and to the thyroid. A complete account of both papers has recently been given by *Robertson* (34).

These authors have taken pains to show that the fatal results are not to be attributed to complications of the operation, or to lesions of the thyroid or of adjacent nerves. But they do not explicitly state that they have histologically examined the tissues removed as parathyroids, and without this precaution it has been my experience that one can never be certain of having actually removed them.

The only other papers which take cognisance of the internal parathyroids were published early in 1897 by *Rouxau*, *Gley*, and *Moussu*; but they do not contain such uniformly successful operations or such uniformly consistent results.

Rouxau (36) performed for the rabbit what *Vassale* and *Generali* had done for the dog and the cat. He removed all the parathyroids, leaving the thyroid intact; and although all the animals did not succumb, he came to the conclusion that in the rabbit this operation is infinitely more serious than removal of the thyroid alone.

Gley (16) repeated the same experiment on 1 cat, 3 dogs, and 9 rabbits, but, in spite of his great experience in such work, he frequently failed to find all the parathyroids, and his results were contradictory. He emphasised the special difficulties to be encountered, and the urgent necessity for histological examination of all structures removed or left *in situ*.

Moussu (28), from his own and from other researches, concluded that two distinct functions exist—the one thyroidal, suppression of which leads only to chronic troubles; the other parathyroidal, suppression of which induces acute symptoms. He also claimed to have induced experimental cretinisms in the dog and cat and in birds by removal of the thyroid, the parathyroids being left *in situ*.

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Parts II. and III. will appear in the succeeding number of this *Journal*.

THE SYMPATHETIC INNERVATION OF THE AORTA
AND INTERCOSTAL ARTERIES. By B. T. TEBBS,
B.A., Queen's College, Cambridge, *Assistant Demonstrator
of Anatomy.*

IN the ordinary descriptions of the distribution of the rami efferentes of the sympathetic system in the thorax, it is stated that the offsets of the lateral ganglia in the upper part of the thorax are distributed to the bodies of the vertebræ and their ligaments and to the thoracic aorta, on which they form a fine plexus, together with filaments arising lower down from the great splanchnic nerve, this plexus furnishing branches to the coats of the aorta and its branches. During a dissection of this portion of the sympathetic system, my attention was drawn to some fine branches from the great splanchnic nerve, ending directly in the coats of the intercostal arteries; and as I cannot find any mention of these branches, I have ventured to publish a note on this occurrence.

The dissection figured in the accompanying figure was made on the right side of the thorax of a subject in the Cambridge dissecting-room. The lateral ganglia were eleven in number, the 7th being particularly large, and appearing to represent two fused ganglia. The great splanchnic nerve arose from the 7th, 8th, 9th, and 10th ganglia, and possessed a well-marked ganglion on its course (ganglion of Lobstein), in the usual situation over the 12th thoracic vertebra. The lesser splanchnic arose from the 10th and 11th ganglia: its method of origin was somewhat peculiar. Two branches, one from the 10th ganglion and one from the 11th, met in a distinct enlargement, placed over the upper part of the 12th thoracic vertebra: from this enlargement the lesser splanchnic proceeded, to be joined lower down by a second root from the 11th ganglion. With the exception of this possible communication between the 10th and 11th ganglia, there was an absolute break in the lateral chain. Such breaks in the continuity of the lateral chain have been recorded by Haller and Bichat. The enlargement on the commencement of the lesser

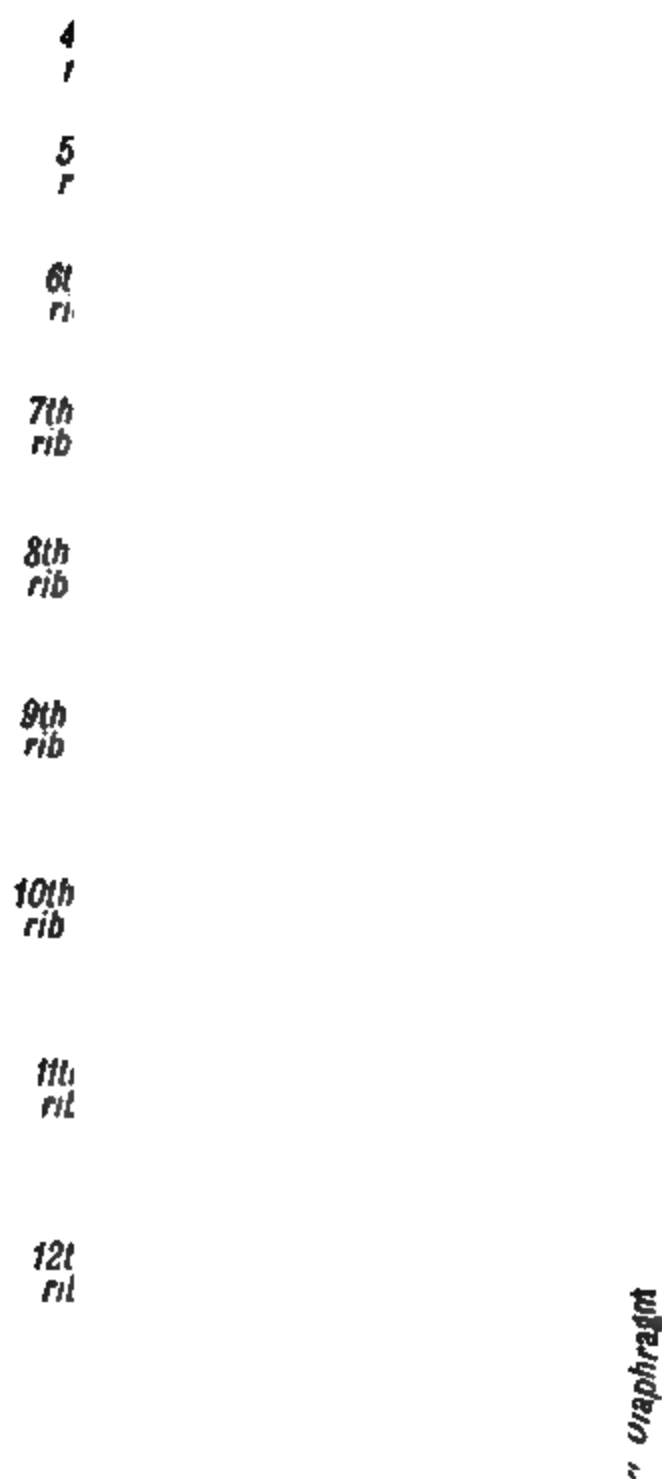


Figure of the innervation of the Intercostal Arteries on the right side.

- a*, Branch from 4th ganglion giving twigs to 1st aortic intercostal artery and to bronchial artery.
- b*, Branch from 5th ganglion to 1st aortic intercostal.
- c*, Loop between 7th ganglion and highest root of great splanchnic giving twig to 4th aortic intercostal.
- d*, Branch from great splanchnic to 5th aortic intercostal.
- e*, Branch from 10th ganglion to aorta and bodies of vertebrae.
- f*, Branch from enlargement on lesser splanchnic to last aortic intercostal.
- g*, Branch from 11th ganglion to aorta and crus of diaphragm.
- h*, Branch from ganglion on great splanchnic to last aortic intercostal, vena azygos, and aorta.
- k*, Communicating branch between ganglion on great splanchnic and lesser splanchnic nerve.
- Lat*, Continuation of lateral chain into abdomen.
- IV*, 4th lateral ganglion.
- XI*, 11th lateral ganglion.

splanchnic may have been ganglionic, since Sperino (according to Hermann and Schwalbe's *Jahresberichte* for 1886) has described cells on the course of the lesser, as well as on that of the greater splanchnic. There was a communicating branch between the lesser splanchnic and the ganglion of the great splanchnic.

The nerves supplying the intercostal arteries in the upper part of the thorax were derived, as far as could be seen, from the lateral ganglia. The 4th ganglion furnished a well-marked branch, directed inwards to the first aortic intercostal artery; and from this branch a distinct twig was given off, accompanying the right bronchial artery which arose from this vessel. A branch was also given off from the 5th ganglion to the same intercostal artery. These branches may have been continued on to the aortic plexus, but unfortunately this could not be traced.

In the lower part of the thorax the intercostal arteries derived a distinct supply from the splanchnic nerves. A distinct branch was found arising from the upper part of the ganglion on the great splanchnic, which gave off a minute twig to the last aortic intercostal,—a large vessel supplying the 10th and 11th intercostal spaces. This twig was traced directly into the coats of the vessel. The rest of this branch was distributed to the vena azygos major and to the aorta. Further, a second branch was given to the same intercostal artery from the enlargement on the lesser splanchnic, which entered the coats of the vessel somewhat farther out. Higher up, a branch was traced to the intercostal, supplying the seventh space from a loop between the 7th lateral ganglion and the root of the great splanchnic arising from that ganglion: this twig also entered the coats of the vessel. The same root of the great splanchnic also furnished a twig to the vessel supplying the eighth space.

The lower part of the thoracic aorta, in addition to the twigs from the great splanchnic, also received branches directly from the lateral ganglia. Two of these branches were traced to it, one from the 10th and the other from the 11th ganglion. The branch from the 10th ganglion was directed inwards over the vertebral column, crossing under the great splanchnic without being connected with it, to end by ramifying over the aorta.

giving a few small filaments to the bodies of the vertebræ. The second branch from the 11th ganglion crossed beneath both splanchnics, and ended by breaking up into a number of fine filaments, some of which ramified on the aorta, while the rest disappeared by piercing the crus of the diaphragm. Lobstein described filaments from the ganglion on the great splanchnic ending in the crus, but Professor Cunningham (vol. ix. of this *Journal*) doubts whether they really terminate here. Unfortunately, these twigs could not be traced further, owing to the abdomen having been dissected; in any case they were very minute, and it would have been extremely difficult to follow them with any certainty. It would therefore appear that the plexus on the lower part of the aorta may be formed by branches from the lateral ganglia as well as from the great splanchnics.

On the left side of the same body I was able to trace filaments to the intercostal arteries from the great splanchnic.

In the subject on which this dissection was made, the supply to the intercostal vessels from the splanchnics and their ganglia appears to be quite well marked; and I hope, by further investigation on other bodies, to ascertain if this supply be constant.

THE LIMB MYOLOGY OF *GYMNURA RAFFLESII*. By
F. G. PARSONS, F.R.C.S., *Hunterian Professor at the Royal
College of Surgeons; Lecturer on Comparative Anatomy at
St Thomas's Hospital.*

SOME time ago Professor Stewart, of the Royal College of Surgeons, gave me the opportunity of dissecting the limbs of *Gymnura*, an animal rarely to be obtained in this country. The myology of this animal has been already carefully described by Dobson,¹ but I make no apology for putting my own dissection on record, because the creature is a rare one, and it is very important that our knowledge of the anatomy of any species should not rest on the dissection of a single individual specimen. In addition to this, systematists regard the dentition of *Gymnura* as being very generalised; and I believe that, as far as its muscles are concerned, it makes the best type of a mammal that I have ever met with. Owing to the work of Dobson, and men like him, we are now able to understand much more of the story which muscles have to tell us than he could hope to do when he wrote his splendid monograph on the *Insectivora*; and I feel convinced that the study of no animal's muscles would form a better introduction to mammalian myology than those of *Gymnura*. In working at carnivores, rodents, and insectivores, one feels that one is close to the main track by which the primates have been evolved from more lowly ancestors, a feeling that is not nearly so strong when one is dealing with monotremes, marsupials, edentates, or ungulates, the muscles of which are more specialised. Few more interesting tasks could be undertaken than to compare the muscles of *Gymnura* and, say, *Bradypus*: in the former their arrangement may often be foretold with great accuracy, in the latter all kinds of unexpected curiosities are met with.

It is, therefore, with the object of confirming Dobson's obser-

¹ *A Monograph of the Insectivora*, by G. E. Dobson, M.A., M.B. London: John Van Voorst, 1882.

variations on this generalised animal that this paper is written: in a few cases we differ as to the interpretation of our observations, while in a few others the observations themselves do not tally; in the latter case the animals may have varied, or one of the observers may have been at fault.

Trapezius.—The occipital fibres of this muscle, as in Dobson's specimen, lie superficial to the cleido-mastoid, and are inserted into the clavicle. The fibres which arise from the ligamentum nuchæ in the neck are inserted with the omo-trachelian into the metacromial process, which in this animal is well developed. The fibres which arise from the anterior three or four thoracic vertebræ continue the plane of the last, and are inserted into the anterior (cephalic) lip of the spine of the scapula. Then there is a wide gap in the trapezius, and the next set of fibres arise from the spines of the posterior two or three thoracic vertebræ and run forwards and outwards, to be inserted into the root of the spine of the scapula as well as into the posterior (caudal) lip of its dorsal third. I think that Dobson's short description agrees with this, though I do not know whether he found the great gap between the fibres coming from the anterior and posterior thoracic spines or not; but it is interesting to me because I have already found a similar gap in the myomorphine rodents occupied by a pad of fat.¹

Rhomboideus capitis et colli (*Rhomboideus anticus*, Dobson).—This muscle, in my specimen, arose from the mesial part of the curved line of the occipital bone as well as from the whole length of the ligamentum nuchæ; it was inserted into the dorsal part of the scapular spine and into the vertebral border of the scapula.

Rhomboideus thoracis (*Rhomboideus posticus*, Dobson).—This is continuous with the last, and arises from the spines of the anterior four or five thoracic vertebræ, to be inserted into the posterior (caudal) part of the vertebral border of the scapula.

Rhomboideus profundus.—This muscle Dobson noticed, but is doubtful as to its name. It arises from the transverse process of the atlas, and soon gains the same plane as the *rhomboides capitis et colli*, with which it is inserted into the dorsal part of the scapular spine. This muscle is often present in mammals, but is in some cases closely united with the levator anguli

¹ "Myology of Myomorphine Rodents," *Proc. Zool. Soc.*, 1896, p. 175.

scapulæ, as in the kangaroos¹ and many rodents.² Windle and I found it quite separate in the Mustelidæ among the Carnivora,³ and we regard it as a deep part of the rhomboid sheet.

Omo-trachelian (Levator scapulæ, Dobson; Levator claviculæ, Acromio-trachelien, and many other synonyms of other authors).—This muscle corresponded exactly with Dobson's description. It arose from the transverse process and ventral part of the arch of the atlas, and was inserted into the tip of the metacromial process. My experience makes me regard this as the most generalised arrangement of the muscle.

Omo-hyoid.—Only the omal attachment of this muscle was present. It was attached to the anterior (cephalic) border of the scapula, close to the root of the coracoid process. This, as far as it goes, agrees with Dobson's description.⁴

Levator anguli scapulæ and Serratus magnus.—These two muscles, as usual, form one continuous plane. The origin in my case was from the transverse processes of the posterior five cervical vertebræ and from the anterior eight ribs.

Subclavius.—This agrees with Dobson's description, coming, as it does, from the cartilage of the first rib, and being inserted into the dorsal border of the outer quarter of the clavicle.

Pectoral muscles.—These agree with Dobson's description, with the exception that I failed to find any clavicular origin.

Latissimus dorsi.—Dobson's description applies perfectly to this. It is interesting to notice that it arises from no ribs, and that its tendon wraps round the teres major, and is inserted ventral to that muscle. *Dorso-olecranal*is (Dorso-epitrochlearis) is as Dobson describes it; this is the typical mammalian arrangement of the muscle.

Deltoid.—Dobson only describes two heads; but as in almost all mammals there are three, I have little doubt that what he described as the clavicular origin of the pectoral was really the clavicular head of the deltoid. This mistake has been made before by writers on myology; but the truth may easily be ascertained by looking for the nerve supply: in *Gymnura*, as in all other mammals that I have examined, the clavicular head is supplied

¹ "*Petrogale xanthopus*," *Proc. Zool. Soc.*, 1896, p. 695.

² "*Sciuromorphic Rodents*," *Proc. Zool. Soc.*, 1894, p. 277.

³ "*Terrestrial Carnivora*," *Proc. Zool. Soc.*, 1897, p. 381.

⁴ The ventral part of the neck was not available for dissection.

by the circumflex nerve. The deltoid of *Gymnura* may be regarded as typical of mammals generally: the clavicular head arises from the outer half of the clavicle, and is inserted lowest down (nearest the elbow) into the deltoid ridge; the acromial head arises between the acromial and metacromial process, and is inserted deep to the last, and further away from the elbow; the spinous head arises from the whole length of the posterior (caudal) lip of the scapular spine, and is inserted deep to the acromial head, and nearer the shoulder joint.

The *Supra-spinatus*, *infra-spinatus*, *teres major*, and *subscapularis* are as Dobson describes them.

The *teres minor* was not differentiated, and I could find no branch of the circumflex passing to the *infra-spinatus*. From the nerve supply of the *teres minor*, one would be inclined to regard it as some of the highest fibres of the spinous part of the deltoid which have acquired an attachment to the subjacent *infra-spinatus* fascia, and so to the axillary border of the scapula; the insertion into the back of the head of the humerus can be understood when one realises that the spinous part of the deltoid is the deepest at its insertion,—i.e., the most posterior of all.

Coraco-brachialis.—Dobson says that this muscle is absent. In my specimen it was also absent on both sides. It is a curious fact that this muscle is entirely absent in certain animals, though others closely allied to them possess it. Of course, the statement of one observer working on one specimen of an animal is not worth much; but in three separate instances I have confirmatory evidence. In the first case I found the muscle absent in the viscacha (*Lagostomus*) on both sides; since then I have come across another specimen in which it was also wanting. In the Libyan polecat (*Ictonyx Libyca*) I found no trace of the muscle; and afterwards Windle dissected a specimen of *Ictonyx zorilla* quite independently, and in that it was absent too. This case of *Gymnura*, in which both Dobson and I have failed to find the *coraco-brachialis*, makes the third.¹ The curious point about it is, that in the chinchilla, closely allied to the viscacha, in the badger and common polecat, close'y allied to *Ictonyx*, and in

¹ Since writing the above, I find that Leche (*Festskrift för Lilljeborg*, 1896, p. 142) has also noticed the absence of any trace of the *coraco-brachialis* in *Gymnura*.

the hedgehog, closely allied to *Gymnura*, a coraco-brachialis is present.

Biceps.—Only the long head is present, as in Dobson's case. This is undoubtedly the most primitive form of the muscle. As far as I know, the coracoid head is never present when there is no coraco-brachialis. The insertion is into the ulna. Macalister,¹ in the kangaroo, describes two parts of the biceps,—coraco-radial and gleno-ulnar. Of these the latter is the more constant, and is the one present in *Gymnura*.

Brachialis anticus.—Only the external part of this muscle is present. It arises from the back of the surgical neck of the humerus, deep to the origin of the external head of the triceps, and winds round the outer side of the deltoid impression to be inserted with the biceps into the ulna. In Dobson's case, however, it went to the radius. Many mammals possess an internal head to this muscle, arising from the front of the humerus; but the one here present is the more constant and primitive.

Triceps.—There are only three heads to this muscle, which answer well to Dobson's description. In many mammals, especially the carnivora, these three heads are subdivided into five or six.

Anconeus.—This muscle has the usual mammalian attachments, that is, the same as in man, except that it is a relatively larger muscle, and is attached to more of the humerus and ulna.

Epitrochleo-olecranalis (epitrochleo-anconeus, Gruber). As is usual in mammals, this muscle is well marked, and lies superficial to the ulnar nerve; its attachments are indicated by its name. It is not described by Dobson.

The *Supinator longus* is absent, as in Dobson's specimen.

The *Supinator brevis* is small and unilaminar, as in all mammals below the Primates.

The *Extensores carpi radiales longior et brevior* are with difficulty separated in their muscular part; the tendon of the brevior is much larger than that of the longior.

Extensor communis digitorum.—This muscle divides into two tendons in the middle of the forearm. Lower down, each of these divides into three slips: the three slips of the outer (radial) tendon go to the 2nd, 3rd, and 4th digits, while those

¹ *Ann. and Mag. Nat. Hist.*, ser. 4, p. 154 (1870).

of the inner (ulnar) tendon go to the 2nd, 4th, and 5th; the slip to the second digit passing deep to those from the radial tendon.

The *Extensor minimi digiti* sends tendons to the 4th and 5th digits, the one to the 4th passing deep to the ulnar slip of the communis to the 5th digit. All these extensor tendons of the fingers unite in a common expansion on the dorsal surface of the proximal phalanx, and are not inserted separately as Dobson describes them.

The *Extensor carpi ulnaris* is inserted into the base of the fifth metacarpal bone, and in every way corresponds to the same muscle in man.

The *Extensor ossis metacarpi pollicis* arises from the back of the ulna as high up as the olecranon process. It is joined by a slip from the supinator brevis.

The *Extensor secundi internodii pollicis* arises from the middle of the back of the ulna. No tendon passes to the index, as in Dobson's specimens. There is, of course, no extensor primi internodii.

The *Pronator radii teres* is large, and passes to the third quarter of the radius. As in all the lower mammals, there is no deep head to it.

The *Flexor carpi radialis* is inserted as usual into the palmar surface of the base of the 2nd metacarpal bone; it is closely bound down to the lower third of the radius. Dobson states that it is inserted into the inferior third of the radius, but it is quite possible that he may have mistaken the fibrous sheath which connects it to that bone for an insertion. This I think the more probable, as the flexor carpi radialis is a singularly constant muscle in mammals.

The *Palmaris longus* is present and large; it ends in the palmar fascia, as in Dobson's specimen. In the description of the muscles of *Erinaceus*,¹ Dobson gives an interesting account of the variations met with in this muscle. Sometimes it is closely connected with the flexor sublimis, sometimes with the flexor carpi ulnaris. In one case, two palmares longi were met with, a condition often found among the carnivora.

The *Flexor sublimis digitorum* arises as usual from the internal

¹ *Insectivora*, p. 50.

condyle; it sends slips to the 2nd, 3rd, and 4th digits, which are perforated in the usual manner. As is usual in the lower mammals, a strap-like loop passes deep to the flexor profundus tendon before the sublimis divides, to allow it to pass through. It is interesting to notice that this strap and the perforated part of the flexor sublimis tendon were found in the theca of the 5th digit, though the rest of the tendon to that digit was suppressed. This arrangement I have met with both in rodents and carnivores.

The *Flexor carpi ulnaris*, as in Dobson's case, arises from the condyle and the inner side of the olecranon; the two heads rapidly unite, and the tendon is inserted into the pisiform.

The *Flexor profundus digitorum* gives a good example of the typical arrangement of this muscle described by Windle.¹ The condylo-radial, condylo-ulnar, condylo-central, radial, and ulnar heads are all present. As is usual, the condylo-central is smaller than the others. The tendon divides into five slips, of which the one to the pollex is joined by a tendinous band, connected at its other end to the palmar ligaments of the carpus. The five heads were found by Dobson.

There are four lumbricales, as in Dobson's specimen. In *Erinaceus* the lumbricales are usually absent or rudimentary.

The muscles of the hand are in a very rudimentary condition. There is a double-headed flexor brevis to each digit, including the pollex; there are no adductors superficial to these, and no interossei dorsal to them.

No thenar muscles are specialised, but there is a distinct and well-marked abductor minimi digiti from the pisiform.

Dobson's description agrees with this, except that he found a partly differentiated abductor pollicis.

MUSCLES OF THE POSTERIOR EXTREMITY.

Gluteus maximus (Ectogluteus) and *Tensor fasciæ femoris*.—These muscles form one sheet, and are inseparable. The origin is from the crest of the ilium, sacral and anterior caudal spines, and the fascia covering the tail muscles; the anterior fibres pass to be inserted into the fascia on the outer side of the thigh, as far as the middle; the posterior run to an ill-developed third

¹ *Journal of Anat. and Phys.*, xxiv. p. 72.

trochanter, just below the great trochanter. Two nerves supply this sheet,—the anterior part by a nerve which emerges round the anterior (cephalic) border of the gluteus medius, the posterior by one winding round the posterior (caudal) edge of the same muscle. The former probably corresponds to the human superior gluteal nerve, the latter to the inferior gluteal.

Gluteus medius (Mesogluteus) has a horseshoe-like origin from the fascia over the tail muscles, from the crest of the ilium, and from the ventral border of the same bone. It is inserted into the diagonal line on the outer side of the great trochanter.

Gluteus minimus (Entogluteus) arises from the external surface of the ilium within the horseshoe-shaped origin of the medius, and is inserted into the anterior surface of the great trochanter. No other gluteal muscles were present, though they were carefully looked for.

Pyriformis.—Dobson says that there is no trace of this muscle. This statement I can quite indorse: absolutely no fibres emerge from the great sciatic notch dorsal to the sciatic nerve, and there is no separate tendon of insertion into the trochanter. The pyriformis is evidently incorporated with the mesogluteus, or not yet differentiated from it.

The *Biceps femoris* (Flexor cruris lateralis) is very large: it arises from the tuber ischii, and is inserted into the lower half of the femur as well as into the fascia of the upper three-quarters of the leg; the lower fibres form a narrow tendon, which joins the tendo Achillis. The muscle is joined by a slip from the semitendinosus, which has a tendinous intersection in it.

The *Tenuissimus* arises by a narrow tendon from the deep surface of the biceps; this soon broadens out into a ribbon-like muscle, and is inserted into the fascia of the lower part of the leg.

The *Semitendinosus* arises by two heads, superficial and deep, the superficial head comes from the caudal vertebræ; part of it joins the biceps as already stated, part unites with the deep head from the tuber ischii. Where these two heads unite in the middle of the thigh, there is, as is so often the case among mammals, a tendinous intersection. The insertion of the semitendinosus is into the cnemial crest of the tibia, at the junction of upper and middle thirds of the leg.

The *Semimembranosus* arises from the fascia over the tail muscles and from the tuber ischii; it follows the typical mammalian arrangement, by dividing into two nearly equal parts, the more superficial of which is inserted into the tibia deep to the internal lateral ligament of the knee, while the deep part or pre-semimembranosus is attached to the femur just above the internal condyle; this part is represented in man by the portion of the adductor magnus supplied by the great sciatic nerve.

The *Quadratus femoris* has a very large origin from the outer side of the tuber ischii: it is inserted between the trochanters on the back of the femur.

Obturator internus and Gemelli.—These muscles have the usual mammalian origins and insertions, but the gemelli are very small. In Dobson's specimen, the obturator internus was absent.

The *Sartorius* (Ilio-tibialis) arises from what should be the anterior (cephalic) end of the symphysis pubis, though, owing to the ill-developed condition of the pubis in *Gymnura*, it is difficult to homologise the parts of it with those of other mammals. The insertion is into the upper part of the cnemial crest of the tibia. I regard this muscle as ilio-tibialis, because it is supplied by the anterior crural nerve.

The *Pectineus* arises from the same place as the ilio-tibialis, but just deep to it: it is inserted into the upper half of the posterior surface of the femur.

There are two *Graciles*, as is the case in many other mammals. The anterior of these arises from the unjoined pubic symphysis, posterior (caudad) to the origin of the ilio-tibialis: it is inserted into the cnemial crest below, and slightly under cover of the insertion of the ilio-tibialis. The posterior gracilis arises from the subpubic arch, and is inserted with the last, but deep to it. In myological literature it is very common to find one of these graciles described as a second sartorius: this is done by Dobson in *Erinaceus*, where the anterior of the two graciles is called 'sartorius alter.' My reason for calling both these muscles 'gracilis' is, that they are both supplied by the obturator nerve. In some mammals the sartorius is double, but it is always supplied by the anterior crural or superior gluteal nerve.

The *Adductor mass* cannot be satisfactorily separated into

layers: it arises from the symphysis and subpubic arch, and is inserted into the whole length of the back of the femur.

The *Quadriceps extensor cruris* presents nothing worthy of special remark. The rectus femoris has two heads, as is usual in mammals, while—a condition which is also usual—the vastus lateralis is greater than the vastus medialis.

The *Tibialis anticus*, as Dobson states, is very large: it arises from the upper half of the tibia, as well as from the fibula. The tendon does not divide, as it does in many mammals: it is inserted into the entocuneiform and first metatarsal bones.

Extensor proprius hallucis.—This muscle agrees with Dobson's description. It arises from the middle third of the tibia, and its tendon passes through the same sheaths in the annular ligament as the tibialis anticus. Close to the insertion of the latter muscle it is bound down by a loop of fibrous tissue, beyond which it runs along the dorsum of the hallux.

The *Extensor longus digitorum* arises, as is usual in mammals, from the front of the external condyle of the femur by a ribband-like tendon. Its tendon of insertion passes through a strong fibrous pulley, which binds it to the calcaneum and prevents it from shifting inwards. It is inserted into the middle and distal phalanges of the four outer toes in the usual manner.

The *Extensor brevis digitorum* was as on the left side of Dobson's specimen. It arose from the calcaneum and sent slips to the four inner toes, that to the first toe being inserted into the proximal phalanx, while the other three joined the tendons of the extensor longus to their respective toes.

Gymnura is an extremely good animal in which to study the peroneal muscles in their most generalised arrangement.

The *Peroneus longus* arises from the head of the fibula and, to a considerable extent, from the intermuscular septa and fascia covering it. It is also in close connection with the external lateral ligament of the knee joint. Its tendon passes down and, at the external malleolus, lies in a groove which is quite distinct from that for the other peroneal tendons, and is situated on the outer side of the malleolus. It then passes across the sole to the base of the 1st metatarsal bone.

The *Peroneus brevis* arises from the upper half of the shaft of the fibula, and passes down in a groove behind the external mal-

leolus, where it lies between the tendons of the peroneus quarti and quinti digiti. As it passes round the malleolus to reach the base of the fifth metatarsal bone, a sesamoid cartilage is developed in the tendon.

The *Peroneus quinti digiti* arises from the upper part of the back of the shaft of the fibula, just below the origin of the peroneus longus. Its tendon passes through the same groove as that of the peroneus brevis, lying to the outer side of that tendon. After it has passed round the malleolus it runs along the dorsum of the fifth toe to join the extensor longus tendon.

The *Peroneus quarti digiti* arises, as is usual, from the fibula below the last. Its tendon passes in the same groove as the peroneus brevis, but on the inner side of it. It is inserted into the extensor longus tendon on the dorsum of the fourth toe.

From my experience of the peroneal muscles of other mammals, I believe that, when all four muscles are properly developed, the peroneus longus always arises highest, and passes through a separate groove on the outer side of the malleolus. The peroneus quinti digiti always arises above the peroneus quarti, and these two pass one on each side of the peroneus brevis in the same groove behind the malleolus.

Dobson says that all the peroneal muscles arise together in *Gymnura* from the head of the fibula, and he describes the peroneus quinti digiti as dividing into two slips for the fourth and fifth toes. I am confident that further dissection would have shown him that all four were really distinct.

The *Gastrocnemius* is large and has the usual two heads, in the outer of which a bony fabella is developed. If the tendo Achillis be examined it will be noticed that, as is usually the case in mammals, the tendinous fibres derived from the inner head pass superficially to those from the outer head, to reach the outer side of the tendon.

The *Soleus* arises from the back of the head of the fibula, and unites with the external head of the gastrocnemius at the commencement of the tendo Achillis.

The *Plantaris* arises in common with the outer head of the gastrocnemius, and passes round the tuberosity of the calcaneum to the sole, where it divides into two layers, the more superficial being the plantar fascia, the original insertion of the muscle, the

deeper being the flexor brevis digitorum, which has acquired a secondary connection with the plantaris, and which goes to the second, third, and fourth toes.

The *Popliteus* arises from the front of a very deep groove on the outer side of the external condyle of the femur: it is inserted into the upper half of the inner border of the tibia. There is no interosseous muscle deep to it.

The *Tibialis posticus* arises from the back of the head of the fibula and runs down in the most internal groove behind the internal malleolus, to be inserted into the navicular bone. This is evidently the same muscle as Dobson's tibialis posticus externus.

The *Flexor tibialis* arises from the back of the inner tuberosity of the tibia, as well as from the inner border of the upper part of the shaft of that bone: its tendon passes through the same groove as that of the tibialis posticus, and in the sole joins the tendon of the flexor fibularis. There can be no doubt that this is the same muscle which Dobson has described under the name of the tibialis posticus internus: the only difference is the method in which the tendon was inserted; in his case it spread out in the sole, superficial to the plantar fascia, and ended in the central callosity of the foot: this seems to me a most unusual insertion for any of the deep muscles of the back of the leg; it is work which the plantaris might be expected to do. Again, it will be noticed that Dobson describes no flexor longus hallucis (flexor fibularis), but says that it is completely fused with the flexor longus digitorum,—a condition of affairs which would make *Gymnura* one of the most anomalous of animals in its leg myology. There can, I think, be little doubt that Dobson either chanced on an abnormal animal, or mistook the insertion of the flexor tibialis. That my specimen of *Gymnura* is normal in the arrangement of these muscles is rendered the more likely, because it reproduces the generalised mammalian arrangement.

The *Flexor fibularis*, which corresponds to Dobson's flexor digitorum longus, arises from the back of the upper two-thirds of the tibia and fibula, as well as from an intermuscular septum on the outer side of the leg, between it and the peronei. Its tendon passes through a groove external to that for the tibialis

posticus and flexor tibialis, and, in the sole, sends off slips for the four outer toes.

There were four *Lumbricales*, but I failed to notice whether their arrangement was the same as in Dobson's specimen.

The *Flexor accessorius* was in my case evidently abnormal: it rose as a perfectly distinct muscle from the anterior part of the external surface of the calcaneum; by flesh; soon after this it narrowed and became tendinous, crossed superficially the long flexor tendons, receiving a small reinforcing tendon from the long flexor mass, and was inserted into the terminal phalanx of the hallux, to which, it will be remembered, no slip was given from the flexor fibularis.

Among the other sole muscles the *Flexor brevis digitorum* has already been described as forming the flexor perforatus of the 2nd, 3rd, and 4th digits.

The *Abductor hallucis* does not arise from the calcaneum, but from the base of the metatarsal bones.

The *Abductor metatarsi quinti* arises from the calcaneum, and ends in the base of the 5th metatarsal bone. This was also noticed by Dobson, who calls it *Abductor ossis metatarsi minimi digiti*.

The *Adductor indicis* was present as in Dobson's specimen.

Double *Flexores brevis* were present in all the five toes, and there were no dorsal interossei at all.

A CASE OF ECTOPIA CORDIS C. FISSURA STERNI.¹

By G. FLEMING BARNARDO, M.B., C.M. Edin.

THE subject of the present communication is a very interesting congenital abnormality, occurring in an otherwise well-formed child, whose clinical history was reported by Dr Graham Grant in the *British Medical Journal*, 5th December 1896, and which was observed by us during the few hours of its life.

On examination some hours after death, the body, which was that of a female child, presented every appearance of health, of being well nourished, and was at the stage of development of a seven month foetus, weighing $4\frac{1}{4}$ lbs. The trunk measured 33 cm.; the upper extremity, from tip of acromion to tip of second finger, measured 19 cm.; the lower extremity, from tip of tuber ischii to tip of heel, measured 17 cm. The umbilicus occupied a position 20.5 cm. from the vault of skull. The chest was flattened antero-posteriorly, and broadened laterally, especially at the lower part. The transverse measurement at the fourth rib was 10 cm.; at the seventh rib, 11 cm. The antero-posterior measurement at the second thoracic vertebra was 5.8 cm., while at the ninth thoracic vertebra 9.8 cm.

The heart was seen lying outside the thoracic cavity, and freely movable, being suspended by a pedicle which springs from the base of the heart and was attached to the thoracic wall. On pressure on the chest there was no resistance indicating the presence of the sternum, and the rib cartilages were noticed to end some distance from the middle line. There was no hernia at the umbilicus. In every other respect the child appeared normal.

Description of the Abnormality.—As above stated, the heart occupied a position outside the chest wall, and was freely movable on a pedicle which attaches it to the thoracic wall. This pedicle contained the aorta, the pulmonary artery and veins, with the venæ cavæ. The general direction of the heart was obliquely towards the left side, with apex pointing some-

¹ Read before the Anatomical Society of Great Britain and Ireland, 1897.

what forwards and upwards, and so placed that the left ventricle is the more anterior. The apex was not bifid, but a distinct sulcus dividing it into two was noticed during life; this was superficial, as subsequent dissection showed. The arrangement of the chambers of the heart was normal, and there was no pericardial sac. The visceral pericardium, as it leaves the wall of the heart, was continued outwards for some distance, and finally blended with the skin of the body generally in a raised margin. The skin here and there invaded this area, rendering the line of junction an irregular one. The shape of this area was roughly ellipsoidal, with the narrow end at the insertion of the umbilical cord, and the broad end blended with the attachment of the pedicle to the chest wall. The heart measured, from the tip of the auricular appendix to the apex, 4.1 cm.; and transversely, from one auricular appendix to the other, 4.4 cm. During life, at each systole, the apex was tilted right upwards so as to touch the child's chin, the heart shortening itself along its long axis at the same time. These movements were very free, and often exposed the child's heart to the risk of injury. In spite of the difficulties under which the heart was acting, the circulation was not much impeded, as there was only very slight cyanosis, and the lungs were not œdematous. Death was probably due to inflammatory processes set up in the heart, as result of its exposed position and the friction of the lint which was put on to protect it.

By dissecting the thorax from behind, one was able to preserve the condition of parts complete in the front of the chest, and so not to spoil the appearance of the specimen. The dissection was carried out by removing the vertebræ mesially, and then separating the two sides of the body. The lungs were normal in structure, each pleural sac occupying its own half of the chest completely, and being in apposition with that of the opposite side along the whole middle line, except at the region of the roots of the lungs and at the upper part of the cavity. It was curious to note that the left lung had a definite tongue-shaped prolongation on its anterior border, such as one generally meets in this situation.

The sternum was found divided into halves, each bar being in relation to the sternal ends of the costal cartilages, and

bounding laterally the opening in the anterior thoracic wall. Their situation is well shown in the figure, as immediately underneath the margin where the skin and the serous surfaces blend. The sternal bars are represented by the narrow strips of cartilage, which are prolonged upwards for a short distance towards the neck, with which the clavicle articulates on both sides. The upper ends of these bars are separated to the extent of two inches, the space being bridged over by a band of fibrous tissue, to which some fibres of sterno-thyroid are attached. The lower ends of these bars are 4 inches apart; the left one is prolonged onwards for a short distance as a projection, remaining free from the ends of the costal cartilages. The right sternal piece has five cartilages in apposition with it; the left, however, has seven. The upper ends of the recti abdominis are separated by a wide interval mesially. The heart was found lying on the central tendon of the diaphragm, and was quite healthy. There was the usual foetal incompleteness of the interauricular septum, but the ventricular septum was complete. The various structures and organs of the child's body were carefully examined, but no other abnormality was found.

Literature contains a considerable number of such cases as the above described, where the ectopia cordis is uncomplicated with other hernial protrusions; but the condition must be looked upon as not very common. It is not, however, so rare among the lower animals, especially birds, as there are several instances recorded, and there are probably many more. The extraordinary thing is, considering the position which the heart occupies in the early stages of the development of the human foetus, that there are not many more cases occurring. All the cases seem very much alike, and one description would almost do for them all. In some cases it is stated that there was no sternum: at the same time, no mention is made of a dissection having been carried out, so that this statement cannot be taken without further proof. The movements of the heart were in all the cases exactly the same; and although in one or two cases the children were born dead or never breathed, others showed every sign of live birth. Every case died, however, soon after birth; in general within a few hours. Dr Braun Fernwaldt, in a recent case, notices that during systole the heart becomes redder than

during diastole, when it becomes pale. This certainly was not the case in the present instance, the reverse being true. There were during systole isolated patches of more marked pallor here and there, but these were taken to be the points of attachment of muscoli papillares, or columnæ carneæ.

Probable cause of Malformation.—The theories advanced differ very materially from each other, and generally tend to explain the condition by supposing some mechanical cause to have been in operation. Now, it seems unlikely that the same cord or the same adhesion could recur with that unfailing regularity as to produce these cases time after time. Barton Cooke Hirst suggests that the exciting cause is an over-distended heart, from increased blood-pressure preventing early closure of the sternal bars. The evidence of this is wanting. Dr Braun Fernwaldt proposes to regard these cases as caused by adhesions occurring between the chest wall of the foetus and the membranes, which leads eventually to rupture of thoracic wall and escape of the heart. That adhesions do occur, and that fairly frequently in cases of abnormal development, lends probability to this suggestion. One of the theories as to the cause of the condition known as extroversion of the bladder rests on an assumption that at an early period the allantoic pedicle becomes fixed by adhesion, and then, when subsequent growth of the foetus occurs, traction is exerted on the umbilicus, and from that point down along the mesial line ventrally, so preventing the complete closure of the abdominal cavity, and leading to a permanent patency of the urachus, and finally to exposure of the cavity of the bladder. There are thus some points of analogy between the production of this condition and that of ectopia cordis. Vrolik suggested that perhaps the closure of the abdominal cavity before the thoracic might tend to leave the heart outside, and so prevent union of the sternal bars. Probably, however, more will be learnt from these anomalies of the true normal process of development, by tracing each anomaly back to the time up to which it was developing normally, and from which it became an abnormality.

The heart is amongst the first organs to be developed, its development occurring at the cephalic flexure during the formation of the amniotic folds, and the closure of the primitive pharynx

into a foregut. The first step in the process is the formation of two coiled tubes, uniting mesially and forming a single tube, which eventually becomes the four-chambered heart. At this early period, while the single coiled tube exists, the heart is very large, and occupies a very prominent position, lying on the umbilical vesicle. This is the condition of parts in a three weeks old foetus. In an embryo 3 cm. long, Ruge showed that chondrification had extended round the body wall, and that from the ends of the seven which are afterwards to become costal cartilages, a series of buds develop, which, uniting, form two longitudinal strips of cartilage: these subsequently fusing in the middle line, give rise to the cartilaginous sternum. This preliminary stage, in which the sternum is represented by two longitudinal strips, is what persists in the present case, and the heart has retained its primitive position. The entire absence of pericardium is not difficult of explanation. On looking at a longitudinal section of an embryo in which the heart is just forming, one notices that the heart is covered by the somatopleure, which is being reflected over the umbilical vesicle as the amniotic fold. Now, if the embryo continues to develop and the heart still remains practically covered by the amniotic membranes,—in other words, forming a hernia into the root of the umbilical vesicle,—then it would only require these to be stripped off during the growth of the child for the heart to be uncovered and left exposed. This being so, one cannot help asking why ectopia cordis is so rare; and if it is rare, there must be some very definite law governing the closure of the body cavity in the thoracic region, which operates with greater regularity than in the case of many other forms of foetal abnormality which are of more common occurrence. The fact that ectopia cordis is more commonly met with amongst birds seems to suggest that perhaps some of the steps in the development of their circulatory system lend themselves more readily to this hernia of the heart.

Those cases in which the heart is within the thorax, with a bifid sternum, might be explained by supposing the disproportionate growth of the heart was not so far in advance, but still sufficient to prevent closure of the sternal bars completely, and that the heart was enabled to retire inside the chest wall, in consequence, subsequently. The association of structural changes

within the heart, such as deficient septa or bifid apex, with ectocardia, lends some support to this view.

I would like to acknowledge here Dr Keith's kindness and assistance; also to thank Professor Windle and Dr Ballantyne for references to the literature.

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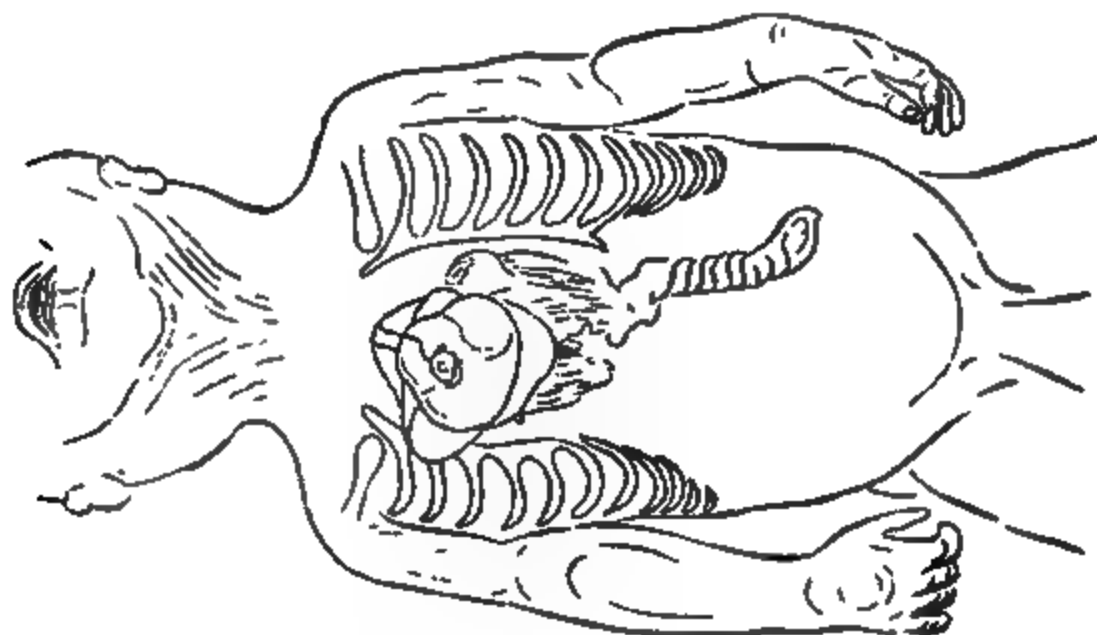


FIG. 1.

FIG. 2.

Diagram showing the relative position of the heart and thoracic wall, as seen by dissection.

THE CAUSATION OF BRACHY- AND DOLICHO- CEPHALY. By Prof. MACALISTER.

It has been cast up as an opprobrium on Physical Anthropology that its literature consists of endless tables of measurements, designated by long and ill-sounding names, compared and combined to form numerous indices; and that, withal, there is very little of a theoretic basis underlying these, or of a principle upon which the selection of measurements depends. The classification of crania is still as arbitrary and empirical as Anders Retzius left it.

In a former communication, read at the Edinburgh Meeting of the British Association, I endeavoured to determine the nature of several influences which act on the growing skull, and which determine its shape. In the present paper I give the results of a few observations bearing on the mechanism of the production of long- or short-headedness.

The skull, which is either long or short, is the brain-case; and the length or shortness of the cerebral hemisphere is correlated to that of the bony case which contains it. There are two alternative conditions of relationship between which we have to choose: either skull-shape determines brain-shape, and moulds the contained organ; or brain-shape determines skull-shape, and is the mould on which the skull is developed. The third possibility, that both may depend on a third independent factor, may for the present be discounted.

There are a few elementary facts which must be borne in mind as fundamental in this inquiry:—

1. That in the early formative period the cranial wall is for the most part soft and non-resisting; and when its bony elements first appear they are separate, and scattered in this soft tissue.

2. When in the human brain the first trace of convolutioning appears at the beginning of the eighth week, the brain-case is soft, and bone is only represented by the ten or twelve tiny specks in the mass of membrane or cartilage. That these convolutions are not due to the growth of the brain surface under

constraint is shown by the fact that by the end of the sixteenth week, although ossification has made considerable progress, yet these primary transitory convolutions have been smoothed out and the surface of the hemisphere has become uniform again.

3. In these early stages the growing surface of the brain is not in contact with the wall of the membranous precursor of the skull. Sections through the foetal head at this early period show that there is a layer of soft fluid-holding embryonic tissue intervening; and that when the cerebral surface begins to grow out at certain spots, these projections jut into the substance of this exceedingly soft precursor of the arachnoid, and do not come at first in direct contact with the more resisting tissue of the skull.

4. The appearance of the surface of the cerebrum at the beginning of the fifth month, when the permanent convolutions are about to form, shows that the surface of the hemisphere is growing unequally: certain areas increase more rapidly than others, and bulge. These bulges are separated by areas of less rapid growth; hence, at first the sulci are wide open valleys, and the convolutions appear as rounded eminences. It is not until the eighth month that the sulci begin to assume the linear character which is distinctive of their later stages.

It is now admitted by all, that the different areas of the cerebral hemisphere are connected directly with the discharge of special functions; and it is a fair inference that, as growth elsewhere is correlated with functional development, so those areas which are earliest to be called upon to work will be among the first to overgrow. Thus the area which presides over skilled movements of the arm develops before that which is connected with similar movements of the leg, even as the arm-bud appears before the leg-bud in the embryo.

It is on the lateral surface of the hemisphere, and especially near to its middle region, that such overgrowths of the surface first appear; and during foetal life it is the central, parietal, and temporal lobes which grow quickest, the frontal and occipital being slower in development. We may expect, therefore, that the infantile head will be in the majority of cases brachycephalic, and so it is. Of twelve British fetuses taken at random, the average index was 80·9, and the range from 76 to 88. Com-

pare with this the average adult English index, which is 74, and ranges from 68 to 82.

This is not limited to British infants: two Egyptian infant heads had indexes of 87 and 80, the average adult index being 75. A Hindu infant's index was 82, the adult average being 75, the highest index of an undistorted Hindu skull known to me being 79. As, up to the period of birth in the average infant, the skull wall is made up of elements which easily move on each other, it is fair to infer that the brain-growth is the determining factor in the early moulding of the foetal skull; and it is characteristic that the part of the infant's head which bulges most at each side is that corresponding to the rapidly growing lower post-central region, where are the areas presiding over the action of the cheeks and mouth, as in sucking, and over the action of the palatine muscles.

Comparing the foetal cerebrum with that of the adult, the most conspicuous points of contrast are: (1) the central or supra-Sylvian height is proportionally smaller, and the temporal or infra-Sylvian height proportionally larger than in the adult. The Sylvian fissure is shorter, and forms a larger angle with the long axis of the hemisphere. The central fissure is shorter, a little farther forward above, distinctly farther forward below, but making a larger angle with the median longitudinal line. The pre-central region is smaller, especially along the line of the horizontal circumference of the cerebrum, and the occipital lobes are smaller.

Turning now to the infant's skull, we note the preponderance of the parietal region, which averages 54 per cent. of the fronto-parietal arc, the range out of 12 taken at random being from 56 per cent. to 52. In the adult, the average parietal element of the parieto-frontal arc is 50 per cent. of the arc, the range of twelve being 52 per cent. to 45 per cent. One result of this is, that in the foetal skull the parieto-occipital fissure lies farther in front of the lambda than in the adult.

As in the average British skull the growth from infancy to maturity is attended with a change in skull-shape, the brachycephalic infant becoming the dolicho- or mesaticephalic adult, some light on the causation of this change may be obtained by tracing the progress of growth. We have seen

that infantile brachycephaly is correlated with shortness of the frontal and occipital lobes, while the parietal, temporal, and central are fairly large. By the end of the first dentition the frontal length has increased, as has the parietal height; and the Sylvian angle has slightly increased, owing to the downgrowth of the central operculum and the base of the third frontal convolution. The post-central gyrus increases, especially at its lower end, and projects beyond, slightly overlapping the pre-central.

By this time skull-growth has entered upon a new phase. Ossification has spread with great rapidity, and before the end of the first year the bones have assumed a definite relationship to each other and suturation has begun to form. From this onward, brain-growth ceases to be free and untrammelled by its envelope, and a contest begins 'twixt brain and bone. The sulci, which hitherto have been open ditches, now become narrowed and linear, and the more rapidly growing gyri tend to overlap their neighbours. As a consequence of this, operculation, which first appears as the result of sheer overgrowth around the insula, now begins to be seen in other portions of the brain: the overgrowing lower post-central region, by its overlap, causes the lower part of the central fissure to be undercut; a similar overgrowth on the medial aspect of the parietal lobe causes it to overlap the occipital along the line of the parieto-occipital fissure, submerging the gyrus cuneii. In monkeys, where the occipital growth preponderates, its overlap produces the *affenspalte*, but in the human brain parietal overgrowth prevents this, and the opercular *affenspalte* never forms. The confusion as to the presence or absence of this fissure in man is due to the two views held as to what is the real *affenspalte*,—whether the chink formed by the occipital operculum, or the deeply submerged transverse occipital sulcus at its fundus.

The growth of the grey surface of the brain from infancy to adolescence is unequal. The first part to increase is the infra-central region and the base of the third frontal convolution; then the superior temporal and the part of the angular gyrus behind it, and the occipital lobe; then, later, the superior parietal and the upper and middle frontal gyri.

The white substance grows commensurately by the increase of

both association and projection fibres, and the brain mass becomes thereby wider and higher. It is, however, only an unproved assumption that the proportion of grey and white matter is necessarily uniform in all parts of the cerebral mass: sectional measurements, specific gravity, and the varying shrinkage in drying, all combine to render it probable that the proportion of grey to white matter is higher in the frontal lobes than elsewhere.

The shape finally assumed by the adult cerebral hemispheres is the result of the interaction of these concurring forces, growth both of the surface and mass of the brain, modified in the later stage by the constraint of the bony case which causes not the convolutioning, but the obliquity of dip of the sulci, and opercular formations.

In the growing English child, the change from brachycephalism to mesaticephalism takes place shortly after the completion of the first dentition. In brachycephalous races, such as the N. Germans, the measurements of the heads of school-children show a slight change about the same time, but often an increase in broad-headedness.

In comparing the cavity of the brain case of a brachy- with that of a dolichocephalic skull, certain differences are manifest to the eye, and numerically estimable by measurements of radial lengths. In order graphically to represent this, I have taken two skulls of the same circumference: one a S. German, with a breadth index of 88; the other an ancient British, whose index is 72. Of these, I have made sections along precisely comparable lines, and drawn these in outline superposed. The skulls of Australians whose brains I have examined would have shown even a stronger contrast, but they were all too low in circumferential length.

In the first section, which is parallel to the coronal suture, and 1 cm. in front of it, the vertical height of the long skull is less than that of the broad, and the radial line drawn through the middle frontal convolution is on one side 13 mm., on the other 15 mm., shorter than that of the broader head. The sectional areas of the included cavity in these skulls are to each other as 25:21.

It is therefore clear that in these two skulls the frontal lobe of the brain of the dolichocephalic skull was smaller in sectional,

probably also in superficial area than the corresponding part of the brachycephalic skull, the enlargement of the latter being above the level at which the horizontal circumference was taken.

Similar sections along the line of the central fissure show a vertical height less by 3 mm. in the longer skull, a radial length taken to the temporal crest of 15 and 10 mm. respectively in the two skulls, the relation of the sectional areas being as 52:44. Sections along the line of the lambdoid suture show comparatively little difference in area.

To show that these are not individual differences, I have taken a large series of radial and other measurements in crania of two groups,—the one of such as had a breadth index of 83 to 85, the other of such as were from 72 to 69 in index. The following table shows the results:—

			Dolicho.	Brachy.
1. Auriculo-metopic radius,	.	.	115	121
2. Auriculo-supracentral,	.	.	128	126
3. Auriculo-occipital,	.	.	101	106
4. Bistephanic width,	.	.	110	126
5. Biparietal do.	.	.	121	132
6. Biasterial do.	.	.	106	112

These numbers speak for themselves.

When, in the course of cerebral growth, the frontal lobes increase in superficial area, then the sectional area of the base of the lobe, which is applied to the front of the central lobe, is of commensurately large size; to this the motor areas forming the central lobe are appended, and subjacent to their cortex run all the association and projection fibres of the frontal lobes. Even if this motor region were not in itself more bulky than in a dolichocephalic skull, it is of necessity wider as being appended to the back of a wider frontal region, and, in turn, its wider hinder sectional area bears the parietal and temporal lobes, whose mass spread over the larger section, becomes necessarily flatter and wider.

All brachycephali are not of the same nature, but at least two types may be distinguished—(1) primary, due to the retention of foetal proportions of the components of the brain, and hence it is a short-headedness accompanied by microcephaly; (2) the secondary brachycephaly is due to increased frontal growth, and usually associated with megalcephaly. The short-headedness

of the Bushman and the Andamanese is of the former type, that of the German is of the latter.

There is an intermediate condition in which brachycephaly of the second type is associated with microsomatism. In these the smaller body is associated with a smaller parietal and central region, while the frontal lobes are larger. There is therefore often a marked shortness of head, but cranial capacity is not necessarily very great. These are often just on the border of megalcephalism: of this nature is the brachycephaly of many of the yellow races.

As in my former paper I dealt at length with the tooth-factor in determining skull-shape, I have not noted it at present, as I desire to direct attention to the brain-factor only. The three other influences, however, of dentition, of muscular attachment, and of balancing, have to be taken into account in any exhaustive study of cranial development.

A CASE OF IDIOPATHIC DILATATION OF THE SIGMOID COLON AND RECTUM, ACCOMPANIED BY A DIAPHRAGMATIC HERNIA OF THE STOMACH.

By E. BARCLAY-SMITH, M.D., *Senior Demonstrator of Anatomy to the University of Cambridge.*

CASES of extreme distension of the large intestine are of sufficient rarity to be recorded when found in the post-mortem room. Extreme conditions of this kind must, however, be seldom met with in the dissecting-room, but by one of those curious coincidences which seem to set the law of averages at defiance, the interesting case described by Professor Howden at the Dublin Meeting of the Anatomical Society, and recorded in the last number of this *Journal*, is promptly partnered by one which came under my observation a few weeks ago in the University dissecting-room.

The subject was a male of 55 years of age, and about 5 feet in height, as far as I could judge. He was markedly scoliotic; the hip and knee joints were in a semi-flexed condition and resisted further extension, although nearly complete flexure of these joints could be induced.

On opening the abdominal cavity in the usual manner, the only object brought to view was a huge loop of gut of very large calibre. This loop, from its general appearance (fig. 1), closely simulated the large intestine as a whole, presenting, as it did, two more or less vertical portions occupying either side of the abdominal cavity, and connected by a transverse piece lodged in the vault of the diaphragm. The whole of this loop, however, was provided with an extensive mesentery, which permitted of its being reflected downwards. On this being done the ascending, transverse and descending colons, together with the small intestines, were found lying behind it, and it became obvious that the loop thus displaced was an exaggeration of the sigmoid portion of the gut.

The descending colon was of normal appearance and calibre. It descended into the left iliac fossa (iliac colon of Jonnesco),

where it was unprovided with a mesentery. In the iliac fossa the gut made a very sudden bend, and becoming provided with a mesentery, ascended vertically in front of the descending colon. In front of the spleen the gut changed its direction, and, passing



FIG. 1.—Represents the appearance presented on opening the abdominal cavity. The transverse part of the loop has descended somewhat from its natural position. *d.c.*, lower end of descending colon. *m.s.*, meso-sigmoid. *B.*, bladder. *l.s.*, sustentacular fold of peritoneum supporting colico-sigmoid flexure. *c.f.*, circular fold of peritoneum surrounding commencement of rectum.

across from one side of the abdominal cavity to the other, described a loop, the convexity of which looked upwards and was lodged in the vault of the diaphragm, coming into close relation with the heart, the position of which was indicated by a very

prominent bulging of the diaphragmatic wall (fig. 2). This part of the sigmoid, however, did not come into direct contact with the diaphragm in the region of the heart, as it was separated therefrom by the great omentum, which was displaced upwards, and, being somewhat folded, constituted a soft pad intervening between the two. After reaching the right side of the abdominal

FIG. 2.—The upper part of the abdominal cavity, viewed from below and in front after removal of sigmoid, &c. *R.l.*, right lobe of liver. *L.l.*, left lobe of liver. *B.*, gall-bladder. *S.o.*, small omentum. *D.*, duodenum (cut). *V.p.*, antrum pylori in left margin of opening into the hernial sac lodged in thoracic cavity. *c.*, bulging of diaphragmatic wall caused by heart. *F.l.*, falciform ligament.

cavity the gut made a second bend in front of the liver (*vide infra*), descended in front of the ascending colon, and, finally inclining obliquely inwards, terminated at the brim of the true pelvis, where the colon ceased and became continuous with the rectum.

The loop of gut, which, between the descending colon on the one side and the rectum on the other, was provided with a continuous mesentery, is regarded in this case as the sigmoid, and

will be thus designated hereafter.¹ The length of the sigmoid was ascertained by means of callipers, measuring from point to point along one of the longitudinal muscle bands (*tænia*), which were conspicuously well marked. Without subjecting the gut to the slightest tension, the result obtained in this manner was a length of 1.13 metres (3 feet 8½ ins.). The dilatation of the gut commenced rather suddenly at the commencement of the sigmoid. From this point the gut increased uniformly in size, reaching its maximum at the point of junction with the rectum. The whole of the sigmoid was filled with semi-fluid contents of a gruel-like consistency. The capacity of the sigmoid was over 3000 c.c. The meso-sigmoid had an extreme length of 18 c.m., with a neck 2.3 c.m. broad: its attachment to the abdominal wall closely resembled the normal.

The rectum also partook of the dilatation, forming a huge cylinder which filled the pelvic cavity to such an extent that pelvic peritoneum was completely deficient. At the pelvic brim the peritoneum lining the iliac fossa on either side was reflected directly on the wall of the gut, and in this situation presented a peculiar circular fold surrounding the line of junction of sigmoid and rectum. This circular fold was continuous on the left with the anterior layer of the meso-sigmoid; on the right it skirted first the right and then the hinder wall of the gut, and became lost in the posterior layer of the meso-sigmoid. The beginning of the rectum was consequently completely surrounded by this circular fold at the pelvic brim. The fold was deepest in front, where the peritoneal pocket between it and the wall of the gut was 3.7 cm. in depth.

There was another remarkable disposition of the peritoneum in connection with the sigmoid, in the form of a fold continuous with the parietal peritoneum on the left side of the descending colon, arched below the angle of junction of the descending colon and the sigmoid, and finally lost rightwards in the anterior layer of the meso-sigmoid, thus constituting a kind of ligamentum sustentaculum for the sharply flexed colico-sigmoid angle.

The fact that the rectum practically filled the pelvic cavity may give an exaggerated idea of its actual size, as the pelvis was

¹ This proviso is a necessity, as anatomists are in a transition stage with regard to the nomenclature and the demarcation into segments of this part of the gut.

much contracted, the sagittal diameter at the brim being 8·5 cm., the coronal diameter 10 cm.

A cast was made of the interior of the rectum. This cast shows that the rectum was funnel-shaped, the apex of the funnel being at the anus. Further, the cast presented a perfectly smooth surface, indicating that the valve-like folds so characteristic of the rectal wall were conspicuous by their absence.

Apart from the great dilatation of the gut exhibited by this case, the chief points of interest in connection with it may be summed up under the following headings:—

- I. The general form and disposition of the sigmoid.
- II. The condition of its walls.
- III. The effects produced on the other abdominal viscera.

I. THE GENERAL FORM AND DISPOSITION OF THE SIGMOID.

In all the recorded cases of dilatation of the sigmoid the form and position of the distended gut bear little if any relationship to the normal. This case, however, may, as far as the general appearance is concerned, be considered as simply an extreme exaggeration of the normal condition. The empty and collapsed pelvic colon (sigmoid) depends in the pelvic cavity, out of which it rises when it is distended with contents, or when it is pushed by the repleted condition of the other pelvic viscera.

In the latter case the higher the sigmoid rises in the abdominal cavity, the more it tends to assume the omega type of loop (Treves). A glance at fig. 1 shows how well the omega form of sigmoid is exemplified by this case. If the surroundings are neglected it might very well serve to illustrate the usual form exhibited by a distended sigmoid of normal size. In this case, however, the loop is enormous, and the position it has assumed is a permanent, and not an occasional or temporary one.

II. THE CONDITION OF THE WALL OF THE DILATED GUT.

There is one noticeable feature in nearly all the recorded cases of dilated sigmoid set forth in the following table (*vide infra*), viz., the wall is the seat of some pathological change. This

change is usually one of hypertrophy, the circular muscle fibres being mainly affected, while the longitudinal muscle bands tend to spread out, and thereby one of the most characteristic features of the large gut becomes lost. Further, the mucous membrane is usually affected, being the seat of more or less chronic inflammation, and is in many cases ulcerated.

In the case under consideration no abnormal condition of the wall of the sigmoid could be found. There was no appreciable hypertrophy of the muscular wall, the mucous membrane showed no sign of ulceration; and although it was examined too long after death to retain any appearance of congestion, yet it certainly showed no thickening, and was to all intents and purposes normal.

Further—and this is one of the most remarkable features of the case—the three *tæniæ coli* were all well marked,—better so than I have usually seen them in this part of the gut. Owing to the presence of the *tæniæ*, sacculation was very obvious.

III. THE EFFECT PRODUCED ON THE OTHER ABDOMINAL VISCERA.

A. *Pelvic Viscera*.—The rectum practically filling the pelvic cavity, the bladder had obviously to find room elsewhere. This viscus had, as it were, become tilted upwards and rightwards out of the pelvic cavity, and lay for the most part in the right iliac fossa (*vide* fig. 1), the neck of the bladder and the prostate lying behind the symphysis pubis.

B. *Abdominal Viscera*.—

(a) The small intestines and the three parts of the colon were normal in calibre and position, although disposed behind the distended sigmoid loop and its mesentery.

(b) *The Stomach*.—On depressing the sigmoid loop and examining the viscera behind, one of the most noticeable features was that no stomach came into view. The absence of the stomach was more apparent than real, as it was found to have retreated from the abdominal cavity into the thoracic, through an enlarged oesophageal opening of the diaphragm. On examining the stomach in the thoracic cavity, it was found to be contained in a true hernial sac, the walls of which were undoubtedly derived from the diaphragm, the frayed-out muscle fibres of which could be distinctly recognised. The summit of

the hernial sac reached the level of the disc between the fourth and fifth thoracic vertebræ. The sac was lined with peritoneum, continuous on the one side with the peritoneum covering the stomach, on the other with the peritoneum lining the diaphragm. The whole of the stomach, however, was not contained in this hernial sac, the antrum pylori being situated in the abdominal cavity. There was a ring of constriction in the gastric wall at the junction of the thoracic and abdominal segments of the stomach. This ring of constriction occupied the aperture in the diaphragm (neck of the hernial sac), and gave an appearance of well-marked bilocularity to the stomach when removed. A gastro-hepatic omentum was present, and this had to a certain extent to pass through the aperture in the diaphragm in order to gain the liver. The œsophagus, which joined the summit of the hernial sac, though much wider than usual, was a straight tube, without any indication of abnormal flexuosity.

Diaphragmatic herniæ of the stomach are rare, and are usually congenital when not the result of traumatism. The condition is usually accompanied during life by marked symptoms, vomiting being a conspicuous feature. In this case, however, as we shall learn later, the condition was not even suspected. The symptoms were remarkable for their absence, and there was no vomiting. The condition, if not congenital, must have been brought about as the result of the distension of the sigmoid, and took place so slowly that the stomach had time to adapt itself to its unusual surroundings.

(c) *The Liver*.—Unfortunately, in most of the cases of extreme distension of the large intestine hitherto recorded, but little notice has been taken of the condition or displacement of the other viscera. The liver, however, is the viscus which of all others seems to most feel the lack of accommodation in the abdominal cavity, and to undergo, as a consequence, the profoundest displacements. Thus, in a case of dilated colon recorded by Rolleston and Haward (*Trans. of the Clin. Soc.*, vol. xxiv. p. 204), the liver was displaced backwards and downwards to such an extent that the under surface together with the gall-bladder looked upwards and forwards. In a similar case recorded by Gee (*St Barth. Hosp. Reports*, vol. xx. p. 19), the liver is described as being pushed much backwards. In Howden's

case (*Journal of Anatomy and Physiology*, vol. xxxii. p. 67), the liver was displaced downwards, rightwards, and backwards. In the present case the liver, which was relatively small, was literally plastered against the posterior abdominal wall to the right of the vertebral column (fig. 2). It was so displaced that when it was exposed the only part brought into view was the inferior surface, as it is usually so described, this surface looking forwards and leftwards. The convexity of the liver consequently looked backwards and rightwards. The liver had undergone such a shifting that the left lobe was the highest part, while the most dependent part was the right lobe, which descended 2.5 cm. below the lower border of the last rib, rested on the quadratus lumborum muscle, on to which the right lateral ligament of the liver was reflected, and ended in a curious tail-like piece which arched round and was in close contact with the outer convexity of the right kidney. The gall-bladder was disposed almost horizontally, the fundus pointing rightwards, and being opposite the ninth rib in the mid-axillary line. At this point the edge of the liver was 12–13 cm. from the right infra-costal margin, the intervening diaphragmatic surface having been occupied in the undisturbed state by the sigmoid. The extremity of the left lobe lay immediately to the right of the œsophageal opening in the diaphragm, and was connected to the diaphragm by a peritoneal fold (lateral ligament), stretching leftwards across the anterior margin of this opening. The falciform ligament was greatly elongated, and stretched downwards, rightwards, and backwards in order to reach the liver.

The liver, from its comparative density, its large size and ample means of fixity, would at first sight appear to be the most stable of all the abdominal viscera. Cunningham and others, however, have taught us that it is one of the most plastic, being readily impressed by the comparatively soft viscera which come into contact with it. Further, this and other cases seem to point out that, as far as position is concerned, the liver is a viscus which readily gives way and suffers displacement in order to afford accommodation for even soft-walled intestine.

(d) *The Spleen* was small, and, as in Howden's case (*loc. cit.*), was deeply placed in the left hypochondriac region.

(e) *Kidneys and Ureters*.—Both kidneys were displaced some-

what downwards, the right more especially. The left ureter was greatly dilated, and just below the pelvis (renal) exhibited well-marked flexuosities. This condition of the left ureter may be accounted for by its having to cross the pelvic cavity in order to reach the bladder (*vide supra*), and in doing so passed between the anterior wall of the dilated rectum and the symphysis pubis. It was consequently in a position when it must have been subject to a considerable amount of pressure during life.

For the sake of comparison I append a table of some recorded cases of distension of the large gut, involving the sigmoid to a greater or less extent;—cases which were not the result of obstruction, and in which for the most part constipation, of longer or shorter duration, was a prominent symptom.

Reviewing the case under consideration, it is apparent that the condition, so far as the sigmoid is concerned, must have been one of extremely long standing. The distension of the gut, retaining, as it did, its normal features and its normal shape, must have been an exceedingly slow process. The severe dislocation of the other viscera must also have taken place very gradually. Much might be learnt from the history of the case, and this we have been fortunate enough to trace through the kindness of Dr Ross. He states that the subject had been under his personal observation for no less than fifteen years. He suffered from paraplegia during this period, and probably for at least forty years, during which time he was an inmate of a workhouse. There was nothing during life to draw attention to any abnormality: nothing was discovered at any rate, *and all the functions of life were carried out normally*. He enjoyed remarkably good health until a fortnight before his death, which was due to an attack of diarrhoea, followed by collapse.

The most remarkable fact about this history is the absence of any suggestion of constipation. Chronic constipation must therefore be eliminated as a factor in the production of the intestinal distension, although it is difficult to conceive that a sigmoid and rectum of such enormous size and capacity and with such relatively thin wall could have brought about normal evacuation of their contents.

To call it an instance of true idiopathic dilatation, although it is more deserving of the name than any other case I can find

Observer.	Publication.	Sex and Age.	Part of Gut distended, &c.	Condition of Wall.	Displacement of other Viscera, &c.
Berry,	<i>Path. Soc. Trans.</i> , vol. xlv. p. 84.	m. 73.	Sigmoid enormously. Gut natural at either end.	Much thickened and ulcerated.	...
Peacock,	<i>Path. Soc. Trans.</i> , vol. xxiii.	m. 28.	From cæcum to upper part of rectum.	Ulcerated.	...
Money and Paget,	<i>Clin. Soc. Trans.</i> , vol. xxi. p. 105.	m. 55.	Colon, but sigmoid chiefly. Rectum moderately.	Marked hypertrophy.	...
Goodhart,	<i>Clin. Soc. Trans.</i> , vol. xiv. p. 84.	m. 17.	Commenced at hepatic flexure and increased uniformly to rectum.	Greatly hypertrophied, ulcerated.	...
Herringham,	<i>St Barth. Hosp. Repts.</i> , vol. xxxi. p. 57.	m. over 70.	Sigmoid enormously. Gut normal at either end.	Much thickened, ulcerated.	...
Gee,	<i>S Barth. Hosp. Repts.</i> , vol. xx. p. 19.	m. 4½.	Sigmoid and rectum mainly.	...	Liver much pushed back. Pelves (renal) and ureters much dilated.
„	m. 4.	Descending colon and sigmoid enormously.
Rolleston and Haward, ¹	<i>Clin. Soc. Trans.</i> , vol. xxix p. 201.	m. 12.	Descending colon. Sigmoid and rectum to a less extent.	Hypertrophied. Long bands spread out.	Under surface of liver and gall-bladder looked forwards and upwards.
Rampold,	<i>Gaz. m.d. de Paris</i> , 1847, p. 831.	f. 76.	From ileo-cæcal valve to anus.	Much thickened, no ulceration.	...
Chambers,	<i>Digestion and its Derangements</i> , London, 1856, p. 496.	f.	A colon of gigantic size (Museum, Christ Church, Oxford).	Greatly thickened.	...

¹ I am much obliged to this paper for several references.

Observer.	Publication.	Sex and Age.	Part of Gut distended, &c.	Condition of Wall.	Displacement of other Viscera, &c.
Houston, . . .	<i>Catalogue of Mus. of Coll. of Surg.</i> , Dublin. Ac. 284.	f. middle age.	Enormous dilatation of sigmoid, 4 feet long.	Much hypertrophied, a few ulcers in rectum.	...
" . . .	Do. Ac. 285.	m. old.	Colon, sigmoid and rectum equally enlarged.	Greatly thickened.	...
Staniland, . . .	<i>Medical Gaz.</i> , 1832.	f. 78.	Colon, sigmoid, and rectum.
Bristowe, . . .	<i>Brit. Med. Journ.</i> , 1885, i. p. 1086.	f. 8.	Colon, sigmoid, and upper part of rectum.	Much thickened and ulcerated.	...
"	m. 24.	Whole of large intestine, but chiefly sigmoid.	Generally hypertrophied.	...
Walker and Griffith, .	<i>Brit. Med. Journ.</i> , 1893, ii. p. 230.	m. 11.	Transverse and descending colon, upper part of sigmoid.	Thickened. Long muscle fibres a continuous coat.	Under surface of liver directed forwards.
Chapman, . . .	<i>Brit. Med. Journ.</i> , 1878, i. p. 566.	m. 58.	Mainly sigmoid.	Uniform muscular coat.	Intestinal sac between diaphragm and liver, which was hollowed instead of being convex.
Fricke, . . .	<i>Brit. Med. Journ.</i> , 1895, ii. p. 1616.	m. 35.	Mainly sigmoid.	...	Heart displaced upwards.
De Haen, . . .	<i>Rab. Medendi</i> , iv. cap. iii. p. 62.	m. 6.	Whole of the large gut.
Parry, . . .	<i>Medical Works</i> , ii. p. 380..	m. adult.	Chiefly colon. Upper part of sigmoid.	Thickened in several parts.	...

recorded, is but begging the question as to the predisposing cause.

That the condition may have been congenital, or at any rate that the tendency to undue lengthening and dilatation of the gut may have been initiated during foetal life, must also be taken into consideration. Two interesting cases recorded by Prof. Hirschsprung of Copenhagen (*Jahrb. d. Kinder K.*, xxvii.) show that this may occur. The subjects were infants of eleven months and eight months respectively, the enlargement mainly affected the transverse colon and the sigmoid, which were hypertrophied and ulcerated, while constipation was a marked symptom from birth. Hirschsprung, I think rightly, considers that the constipation in these cases was secondary to the dilated condition of the gut, acquired during foetal life, and to be explained by faulty development.

The long history of paraplegia may, however, have an important bearing upon the present case, and I feel inclined to fall back on Dr Angel Money's suggestion (*Clin. Soc. Trans.*, vol. xxi. p. 106), and to regard it as due to an obscure nerve lesion. The disturbance of the central nerve system probably resulted in a gradual loss of tonicity of the muscular wall of the gut. This loss of tonicity was accompanied by a very gradual lengthening of the muscle fibres, with a consequent increase in length and calibre. The gut, however, seemed to have reacted to the altered condition of its walls, and was always capable of normally evacuating its contents.

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Fig. 5



sex-gland

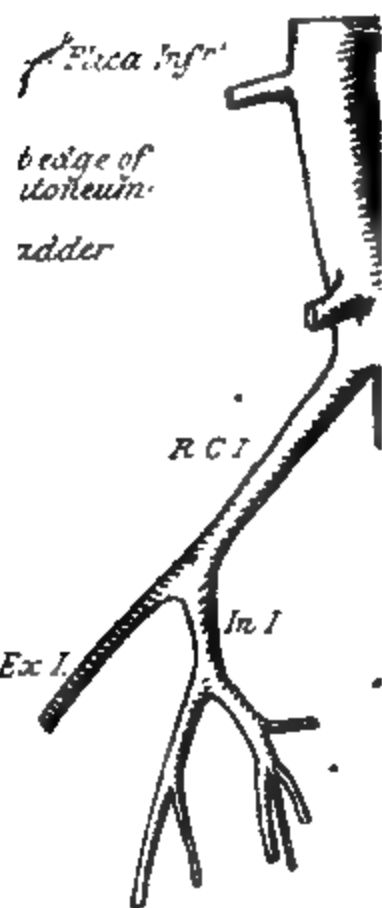


Fig. 6.

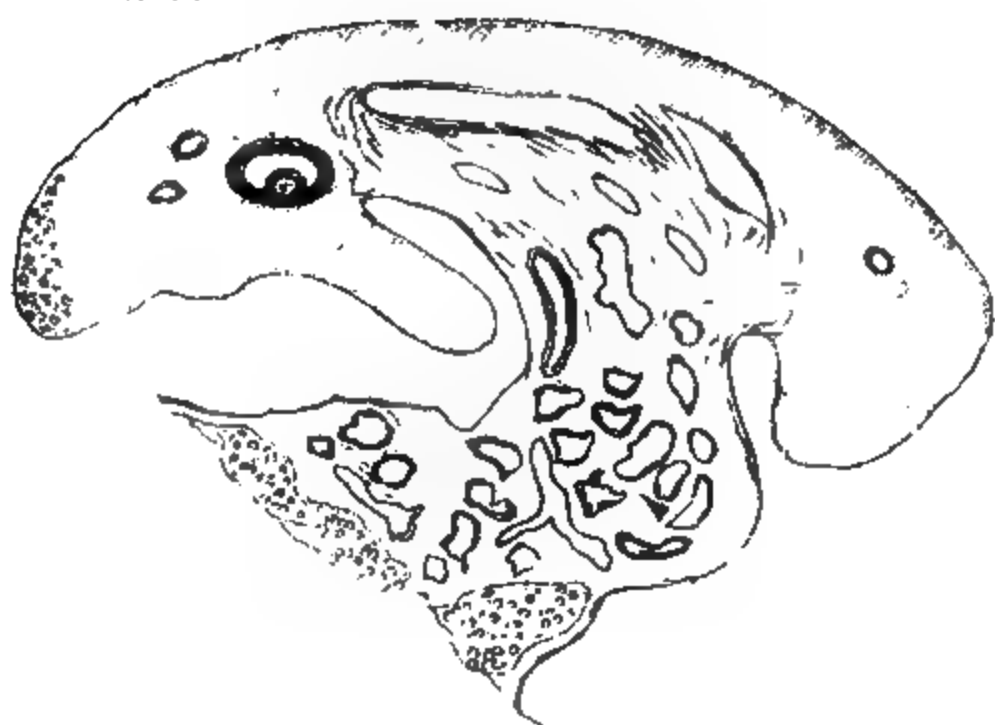
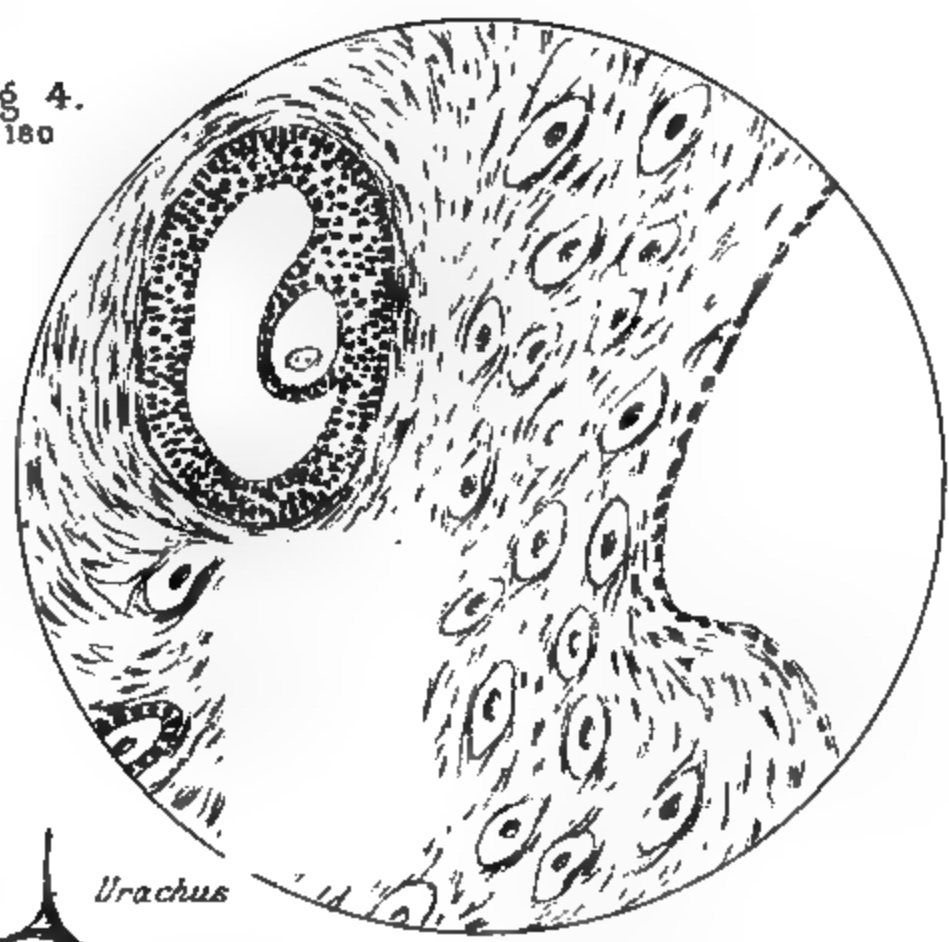


Fig 4.
 x 180



2.
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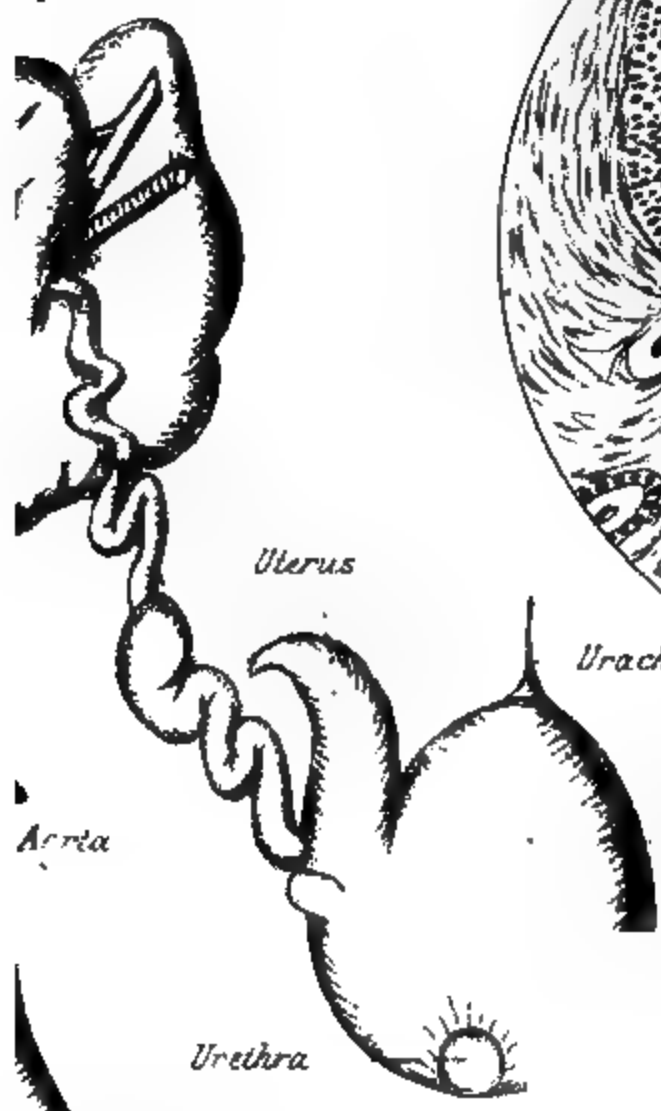
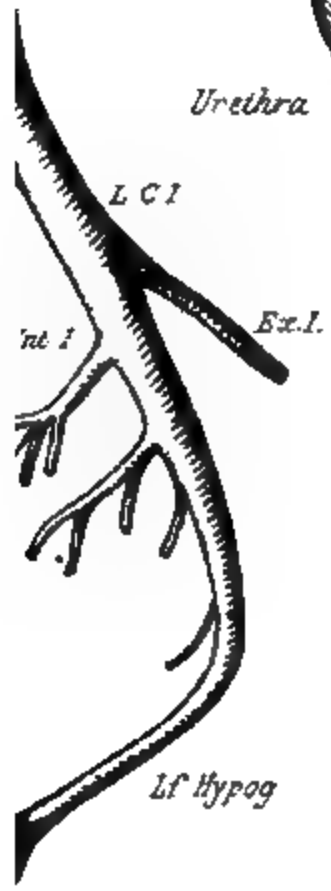


Fig 5.
 x 180



Journal of Anatomy and Physiology.

A DECORATED SCULPTURED HUMAN SKULL FROM NEW GUINEA. By Professor Sir WILLIAM TURNER, F.R.S.

IN April 1895 one of my pupils, Mr F. N. Johnston, M.B., presented me with a skull which had been given to him by a friend living in Queensland, Australia, but he could not tell me the place in which it had been collected. As it did not conform with the customary characters of the skulls of the aborigines of Australia, and as it showed a remarkable decorative sculpturing of the frontal bone, I put it on one side to await further light on the specimen.

In the month of October 1897 I received, through the courtesy of the authors, a copy of a memoir entitled "Observations on a Collection of Papuan Crania," by Messrs G. A. Dorsey and W. H. Holmes,¹ in which they describe a series of sixteen decorated skulls from the hut of a native chief, who used them for the adornment of his house, and prized them as trophies of war. Eight of the skulls were apparently men, seven women, and one a child from 8 to 9 years old. Although the information regarding the locality from which these crania were obtained is not so precise as could be desired, it seems probable that they were collected by a sea-captain in the vicinity of some of the ports in the island of New Guinea, on the northern shore of the Papuan Gulf, in the British protectorate.

As my specimen bears a general resemblance in its form, in the character of the sculpturing, and in the mode of connection of the lower jaw and teeth to the skulls described by Messrs Dorsey and Holmes, I believe it to be from the same or an

¹ *Field Columbian Museum*, publication 21, Anthropological series, vol. 11, No. 1, Chicago, August, 1897.

adjoining locality. The proximity of the coast of New Guinea to the colony of Queensland would readily allow a skull from the former island to find its way into the hands of a Queensland colonist.

The skull in my possession had evidently been preserved for some time in the house of a native, for the cranium at its back, sides, and base was blackened with smoke, but the bones of the face had been smeared with a red pigment. It was that of a man apparently in the prime of life. The sutures were unossified, and the teeth were moderately worn.

In the *norma verticalis* the roof was ridged in the sagittal line, and sloped steeply outwards to the parietal eminences, which, as well as the frontal eminences, were not protuberant. The side walls of the cranium were almost vertical in each region, and the zygomata were not visible when the eye was fixed on the bregma. The general form was an elongated oval, and the breadth was small in relation to the length, so that the skull was hyperdolichocephalic, its length-breadth index being only 68.

In the *norma lateralis* the glabella and supra-orbital ridges were feebly marked, the fronto-nasal depression was shallow, and the osseous bridge of the nose was moderately projecting.

The upper jaw projected well forwards in the incisive region. The nasal spine of the superior maxillæ was moderate, and the floor of the nose was not separated from the incisive region by an intermediate ridge. The diameter from the basion to the junction of the nasal spine with the floor of the nose was 95 mm., whilst the distance from the basion to the alveolar point was 101 mm., measurements which indicate the degree of alveolar prognathism.

The forehead was not very receding, and its curve was continued backwards into the arch of the vault. From the obelion to the occipital squama the vault sloped gently downwards and backwards. The temporal curved lines and the nuchal region of the occiput were distinct, but the mastoids were not massive. The parietal longitudinal arc was the longest, and the occipital the smallest. The basi-bregmatic diameter was distinctly higher than the greatest breadth, and the length-height index was 71.9. There was a large epipterice bone in the left pterion, and a small triquetral bone in the left lambdoidal suture.

The nose was moderately platyrrhine. The orbits were markedly microseme, although the bones forming their boundary on the face were not tumid. The palate was almost as long as broad, and distinctly dolichuranic. In the proportion of interzygomatic breadth to nasio-mental length the face was low, and came into the chamæproscopic group of Kollmann.

In the feebly projecting glabella and supra-orbital ridges, in

FIG. 1.—Both figures are reproductions of photographs by Mr W. E. Carnegie Dickson.

the forehead not being very receding, in the shallowness of the depression at the root of the nose, in the moderate projection and only slight flattening of the nasal bridge, and in the want of tumidity in the base of the orbit, and the comparative lightness of the skull, the specimen was obviously not that of an aboriginal Australian. On the other hand, the elongated, narrow cranium, with the low length-breadth index, the basi-bregmatic diameter being greater than the parieto-squamous, the microseme orbits,

the projecting upper jaw, and the somewhat platyrrhine nose, showed its affinities to the Melanesian or Papuan race, to which I have no doubt it belonged.

The most interesting features in the specimen were the decorative sculpturing on the frontal bone, and the arrangements for

FIG. 2

securing the lower jaw to the skull, and for retaining the teeth in their place. The frontal sculpturing was included in an area 71 mm. wide and 61 mm. in vertical diameter, immediately above the glabella and supra-orbital ridges. It had been produced partly by scraping and partly by incising the outer table of the

frontal bone with a more or less sharp instrument. It consisted of a central figure enclosed in a sort of frame, from the latter of which a number of short lines were cut, directed inwards towards the figure. When the latter was looked at in the natural position of the skull, it was somewhat difficult to determine its significance. When the skull was reversed, the figure was then seen to be a rude representation of a face, apparently human, which had been engraved upside down. Two eyes and a pair of eyebrows were immediately above the glabella, a long straight nose, upper and lower lips, an open mouth, a series of short incised lines to represent teeth, and a tongue, could all be recognised. On each side of this rudiment of a face an elongated, curved, limb-like object had been cut in the bone, the exact signification of which it was difficult to determine, though it undoubtedly outlined the face with more distinctness.

The lower jaw was securely fastened to the skull. Through each ascending ramus a hole had been bored, and a piece of split cane had been passed through it and secured around the zygoma. Pieces of split cane had also been passed through the nose immediately above the floor, and carried out of the posterior and anterior nares around the back of the palate and symphysis menti, in front of the latter of which they had been secured by a series of knots. The necks of the teeth in each jaw were enclosed in loops of string formed of some vegetable fibre, which secured them together and retained them in their sockets. The mode of fastening the lower jaw and of securing the teeth was on the same plan as that described and figured by Messrs Dorsey and Holmes in their series of crania. In a skull from Warrior Island, Torres Strait, which I described and figured some years ago,¹ the lower jaw is secured to the skull by a naso-mental cord of vegetable fibre, and a similar cord connects on each side the neck of the jaw to the zygoma: the ramus is not perforated, and there is no string around the necks of the teeth. This skull is hyperbrachycephalic. It is exceptional to find in the skulls collected in New Guinea the lower jaw attached to the cranium. This is explained by the Rev. Dr Macfarlane, who was long resident as a missionary in the island, as due to the fact that in their head-hunting expeditions the lower jaw is the trophy

¹ *Journal of Anatomy and Physiology*, vol. xiv., July 1880.

claimed by the man who first wounds the victim, whilst he who kills and beheads the slain acquires the skull. There are two separated lower jaws from New Guinea in the University Museum, in which a cord had been tied across from the neck on one side to that of the other, so that the jaw could be worn as a bracelet.

Although the series of sixteen decorated crania described by Messrs Dorsey and Holmes were all sculptured in the frontal region, in none was the design the same as in my specimen, and, indeed, in no two of their series were the patterns alike. It would seem, therefore, that each artist trusted to his own ingenuity in making a design, and did not copy either himself or his neighbours. Mr Holmes, in his chapter on the drawings, states that nearly all embody easily distinguished animal forms: and though the more formal examples approach the purely geometric, they "are also doubtless animal derivatives, or representations of land, water, or other natural phenomena." In none of his specimens had any attempt been made to delineate the human face, and in this respect the skull now described is peculiar and interesting.

Professor Haddon, in his elaborate memoir on the decorative art of British New Guinea,¹ gives careful descriptions and figures of numerous designs which he has studied. He refers to the realistic or suggestive character of the decorative art of the natives, and the frequent copying of natural objects. He has found representations of the human form on articles brought from the islands in Torres Straits, and from the Fly River district. The region in which the human face, or designs derived from it, seems to be most frequently employed for decorative purposes is, however, that of the Gulf of Papua, so that it is not unlikely that the skull which I have now described came from some part of that seaboard; and I may especially refer to a face depicted² on a belt in the Berlin Museum (VI. 6745), as closely approaching in design that sculptured on the forehead of my specimen.

As a further contribution to the craniology of New Guinea, I have given in the table on page 359 measurements of a skull which was presented to me in 1890 by one of my Australian

¹ *Cunningham Memoirs of the Royal Irish Academy*, Dublin, 1894.

² See Haddon, *op. cit.*, p. 115.

pupils, Mr L. J. Lamrock. It was obtained from a hut at Port Moresby, in which it had been hanging for a number of

	Sculptured Skull.	Port Moresby.	Jarvis Island, Torres Strait.	Warrior Island, Torres Strait.
Collection,	E. U. A. M.	E. U. A. M.	E. U. A. M.	E. U. A. M.
Age,	Ad.	Ad.	Ad.	Ad.
Sex,	M.	F.	M.	M.
Cubic capacity,	1190	1140	1230	1534
Glabello-occipital length,	178	174	178	175
Basi-bregmatic height,	128	132	130	137
<i>Vertical Index</i> ,	71·9	75·9	73	78
Minimum frontal diameter,	94	87	90	103
Stephanic diameter,	101	97	105	122
Asterionic diameter,	106	103	106	120
Greatest parieto-squamous breadth,	121·s	121·p	130·s	154
<i>Cephalic Index</i> ,	68·0	69·5	73	88
Horizontal circumference,	491	480	494	515
Frontal longitudinal arc,	122	121	122	130
Parietal " "	135	122	132	135
Occipital " "	104	110	106	109
Total " "	361	353	360	374
Vertical transverse arc,	277	286	280	330
Length of foramen magnum,	34	30	31	36
Basi-nasal length,	97	104	99	105
Basi-alveolar length,	100	110	108	107
<i>Gnathic Index</i> ,	103·1	105·8	109	102
Interzygomatic breadth,	118	116	122	140
Intermalar,	109	99	113	125
Nasio-mental length,	101	116
<i>Nasio-mental complete facial Index</i> ,	85·6	82·8
Nasio alveolar length,	61	71	68	65
<i>Maxillary upper facial Index</i> ,	51·7	61·2	55·7	46·4
Nasal height,	46	54	46	47
Nasal width,	24	24	24	24
<i>Nasal Index</i> ,	52·2	44·4	52·2	51
Orbital width,	40	38	39	45
Orbital height,	30	34	29	31
<i>Orbital Index</i> ,	75	89·5	74·4	68·9
Palato-maxillary length,	57	60	65	64
Palato maxillary breadth,	60	55	62	69
<i>Palato-maxillary Index</i> ,	105·2	91·6	95·3	108
Lower Jaw. { Symphysial height,	23	33
Coronoid " "	59	74
Condylod " "	54	70
Gonio-symphysial length,	85	95
Intergonial width,	90	103
Breadth of ascending ramus,	31	40

years, and was said to be that of an old woman, who had been a witch in her tribe.

This skull was without the lower jaw, and was black with smoke. It was without doubt that of a woman. The teeth had all been lost, but the sockets were unabsorbed, though those of the right hinder bicuspid and the true molars were broken away. The sutures were unossified, and were remarkably simple. The cranium was an elongated oval, narrow in relation to its length, and hyperdolichocephalic, with an index 69.5. Its height followed the rule in Melanesian crania in being greater than the breadth, the vertical index being 75.9. The frontal and parietal eminences had the prominent female sexual characters, and the vertex was more flattened than in the decorated male Papuan previously described. The forehead was almost vertical; the glabella and supra-orbital ridges were distinct; the fronto-nasal depression was shallow; the nasal bridge was somewhat flattened; the nasal index was leptorhine, a character which was due to the unusual nasal height for a Melanesian skull. In consequence of the marked vertical diameter of the superior maxilla, a high upper facial index (leptoprosopic) was obtained. The orbits were megaseme; the gnathic index was strongly prognathous; the nasal spine of the superior maxillæ was moderately prominent, and the floor of the nose passed into the incisive region smoothly and without a ridge of separation. The diameter from the basion to the base of the nasal spine was 98 mm., whilst the basi-alveolar diameter was 110 mm., which produced distinct alveolar prognathism. The palato-maxillary diameter was long, and it is remarkable that the length somewhat exceeded the breadth. The glabella and supra-orbital ridges were marked by a few incised lines, running vertically but quite irregularly and without a pattern. A third condyl was present on the basi-occipital.

I have repeated in the table measurements of a dolichocephalic cranium from Jarvis Island, Torres Strait, which I gave in my Memoir on the skulls of the "Challenger" collection,¹ and by way of contrast, those of the hyperbrachycephalic skull from Warrior Island, Torres Strait, already referred to. In that memoir I analysed the measurements of the numerous crania from New

¹ *Challenger Reports*, part xxix., 1884.

Guinea which had up to that time been recorded by a number of observers. Two distinct types of skull have been met with,—a brachycephalic, in which the breadth of the cranium, as a rule, exceeds the height; and a dolichocephalic, in which the height usually exceeds the breadth. The skulls, the description of which is given in this communication, are hyperdolichocephalic, and the vertical index is higher than the index of length and breadth in both of these crania.

AN ACCOUNT OF A BLASTODERMIC VESICLE OF
THE SHEEP OF THE SEVENTH DAY, WITH TWIN
GERMINAL AREAS. By RICHARD ASSHETON, M.A.
(PLATE VI.)

IN view of the great interest which is taken in the question of the origin of homologous twins, and the many forms of abnormality which are supposed to result from the more or less complete fission of the embryo at an early stage, I fancy that an account of a specimen of a very young mammalian blastocyst with two germinal areas may be worthy of notice.

Hitherto cases of early double embryos have been apparently very seldom met with among mammals. So far, I have been unable to find any instance recorded of a double germinal area on the blastodermic vesicle.

In every work which treats of the origin of twins and double monsters that I have consulted, I fail to find instances of mammalian double embryos, and I find that all theories advanced are based almost entirely upon avian, amphibian, or piscine examples. By far the greater number of instances given are avian.

From the time of Wolff until the present day, many instances of naturally-produced double embryos of the chick have been recorded, and many of them carefully described.

In a list which I give at the end of my paper, which is chiefly compiled from Dareste's work (8), it appears that the recorded cases in birds' eggs of either two perfect embryos on one yolk, or of double monsters in various states of union, amount to less than ninety specimens, which is really not a large number considering the enormous number of eggs which are opened in the laboratories at early stages. Of this number, no less than 55 are recorded by Dareste, though in his case—which may also be true of many others—it is doubtful whether one can describe the specimens as naturally produced, since the majority would

seem to have occurred during incubation under abnormal conditions, as, for instance, in a lowered temperature.

Among these are included cases of three embryos on one yolk in the bird's egg.

I have myself opened a large number of eggs during the last ten years, but can only recollect one case of a double embryo. I have also opened some hundreds of sparrows' eggs, but I have never come across a double embryo. The only abnormality in the sparrow embryo that I have noticed was the absence of the amnion in a specimen equivalent to about a six or seven day chick, which had led to certain slight deformities.

It is well known that cases of double monsters are not uncommon among fishes, and that they occur more frequently in artificial fertilisation than in the natural course, and are still more frequent in the dry than wet method. In recent years double embryos have been artificially produced by many workers in amphibians, and other groups of chordate and invertebrate animals.

But it is to the avian instances that most attention has been paid; and around them, in the absence of mammalian cases, the controversy has from time to time been carried on as to whether the formation of double monsters occurs by fusion of two separate germinal vesicles, or by a fission of one primary area. The specimen I am about to describe proves, I think, conclusively that a fission of the embryo at a very early stage does occasionally occur in mammalia under normal circumstances; and it is in this case clearly a matter of how far apart the two embryonic masses may be at the time of the formation of the amnion and placenta whether they will produce twins or a double monster, provided, of course, that each germinal mass is in itself, as it appears to be in my specimen, a perfect embryo.

Fig. 1 is a surface view of the specimen, showing the positions of the two embryonal areas at A and B.

The circumstances under which the specimen was obtained were as follows.

A pure-bred Lincolnshire ewe was served by a pure-bred Lincolnshire ram on 22nd November 1897, and the ewe was killed on the afternoon of the 29th of the same month, or about one week after sexual union.

The age, therefore, of the specimen did not exceed seven days. The time which elapses between sexual union and the impregnation of the ovum in the sheep is, however, subject to some variation.

There were signs of the discharge of two separate ova from one of the ovaries. I only found this one specimen, which was obtained from the horn of the uterus in connection with the ovary showing the two corpora lutea.

Anyone who has attempted to find the early embryos of the sheep will know how difficult a task it is, and will not be surprised that I found but one specimen out of the two expected on this occasion.

The usual shape of the blastodermic vesicle of the sheep at this stage is oval, with the embryonic area upon the less convex surface. In the present instance, the blastodermic vesicle was more spherical. It was not, however, by any means regular in shape; its walls were flaccid, as is always the case after the rupture of the zona radiata.

For a further description of the normal stages of the sheep's development, I may refer to my paper in the *Quarterly Journal of Microscopical Science*, vol. xli., which will shortly appear, in which I describe fully such specimens as I have, and the manner of obtaining them.

Suffice it at present to say that this specimen was hardened by .5 per cent. chromic acid, stained all night in carmalum, and cut and mounted as a series of sections .005 mm. thick.

An examination of the sections shows that, as far as I am able to judge, both embryonic areas are complete. But I am the more confident in the case of the one, A, than the other; because in the case of B, a stage seems to be represented which I have not hitherto met with in my ordinary specimens.

Fig. 2 represents a section through the specimen taken along the line a-b in fig. 1. This section cuts the edges only of the two embryonic areas. I have drawn this for the twofold purpose of showing the actual and relative positions of the two areas on the blastodermic vesicle, and of indicating the extension of the inner or hypoblastic layers, H B, H A, of the two embryonic masses.

The adjoining outline figures A and B represent the median sections of the respective germinal areas, drawn to the same scale as fig. 2.

It should be stated at once that there was nothing either in the surface view or in the section to suggest a fusion of two separate blastocysts; but to this I must refer again.

The true hypoblast layers, H A, H B, are seen to be quite separated from each other; in fact, the embryos are connected only by the trophoblast or main wall of the blastocyst, no portion of which is retained after foetal life.

The area A differs only from a normal one in being very distinctly smaller.

Fig. 3 is the seventh section of a series of sixteen which pass through the germinal area A. It may be compared with the outline figure 5, which represents a median section of the embryonic area of a normal embryo of the sheep, of what I take to be the corresponding age.

The conditions of the two embryonic areas are alike; and the extension of the hypoblast, away from the epiblastic knob, is about the same in each case. If the two specimens represent the same age, it is clear that the difference in size is great, amounting to nearly double. But it is, of course, possible that fig. 5 represents an older stage than fig. 3. A glance at the latter figure will give the relations of the epiblast E, of trophoblast T, and hypoblast H. It will be remembered that the earliest sheep embryo hitherto described is that figured by Bonnet (3), in which there was no trophoblast overlying the permanent epiblast.

It may be noticed that although there is so great a difference in size between the two areas, figs. 3 and 5, yet the nuclei are approximately equal. The difference in size is due to a lesser number of cellular units in the one case, and not to a reduction in size of the several cells and their nuclei.

In the other embryonic area B, which is rather smaller than A, the condition of things shows a slight advance upon that of fig. 3. Fig. 4 is the seventh section in a series of twelve which cut the area B.

The hypoblast H, as represented in fig. 3, consists of a thin layer of attenuated cells applied to the inner surface of the

embryonic epiblast E, but it shows a more marked discontinuity with the trophoblast than it does in fig. 3.

The epiblastic mass E is distinctly flatter, and instead of being covered over its whole outer surface by the trophoblast T, it is naked in its more central area, and exposed to the surface X.

In the section which I have drawn, and perhaps in the one which follows, there may be seen to be what is, I believe, a small pit in the centre of the exposed surface of epiblast X.

It must be extremely narrow; for although the section drawn is slightly thicker than the others, it is not likely that it exceeds $\cdot 0065$ mm. in thickness.

If this be a pit, it will no doubt be the commencement of some process such as is found accompanying the rupture of the trophoblast layer in many other mammals,—*Tupaia* (Hubrecht, 11); *Talpa* (Heape, 10); *Sus* (Weyssse, 12, Assheton, 2), etc.

In that case this embryonic area is of special interest, as it represents a stage between the oldest specimen described by me (1) and the youngest found by Bonnet (3).

Whether this be a pit or no, the trophoblast layer is evidently absent from the centre of the epiblastic area, so that I think I am justified in assuming that in the sheep the trophoblast layer ruptures over the true epiblast, and remains in connexion with its edges only, as is known to be the case in certain other forms. So, although I have no other specimen with which to compare it, yet considering what is known to occur in other mammals, it seems to be quite possible and probable that this embryonic area B is in all respects perfect, except that it is only half the size of a normal specimen.

At certain places—but by no means forming a continuous layer—I find a thin lightly-stained layer, marked Z in the figures 3 and 4, which may be remains of the zona radiata; which, however, I have never seen in so large a blastocyst of the sheep. The zona radiata usually disappears at an earlier stage, though not an earlier date. Nor is it quite like a zona radiata, because it has not stained deeply as a zona radiata usually does with carmalum. Possibly it is not the zona radiata, but a mucous deposit derived from the uterus, and should be compared with the ‘prochorion’ of Hensen, recently described in the dog by Bonnet (5).

From the above description we may conclude that in this specimen there are two germinal areas upon one blastodermic vesicle, each apparently perfect, and presumably capable of forming a perfect embryo. They are completely separated; and from what is known of the extraordinary expansion of the normal blastocyst of the sheep, there would have been nothing to prevent the two germinal areas becoming so far removed from one another as to make interference with each other almost impossible.

It is clear that in this case each embryo would have a separate and complete amnion of its own, and at the close of foetal life might have had no other connexion than that which normally occurs through the expansion of the allantois when two originally separate embryos develop in the same uterus.

It is also interesting to note the difference in size between the two germinal areas, as well as the difference in the state of development. In this case it is the smaller of the two which has obtained a start upon the other, and both are much smaller than might be expected from their stage of development; from which it would seem possible that size has much to do with the stage of development.

It will have been gathered from my comparison of the twin specimens with my normal ones that I should not have expected to find either germinal area so far advanced as it is. Subject to the great uncertainty as regards the actual age of normal specimens, I may say that I should have expected the area A to be a nine-days embryo, and the area B to be a ten-day or even an eleven-day embryo; instead of which, they are certainly not more than seven days old. The difference in the stage of the two embryos is not perhaps very great, but it is sufficient to show that at a very early stage one may get a start of the other, which might lead to the partial absorption or even to the inclusion of the one less advanced, if not far removed. (Compare Duval (9), fig. 8 (*Schéme de la production des monstres endocymiens*)).

There were, as I mentioned in the earlier part of this paper, evident signs in the ovary of the discharge of two ova. This fact, with the finding of one double blastocyst, might tempt

some to suppose that it was a case of fusion of two originally separate blastocysts.

The following considerations, I think, are enough to dispose of such an explanation.

Firstly, each germinal area is undoubtedly much smaller than the normal germinal areas of the corresponding ages.

Secondly, there is no trace of a line of fusion. It is extremely unlikely that they should fuse as long as the zona radiata is intact. As the zona radiata can have only quite recently ruptured, the fusion must have occurred, if it did occur, very recently; but of this no sign exists.

Thirdly, there is no evidence, so far as I know, of the fusion of blastodermic vesicles. In the pig, for about the fourteenth to twentieth days, there may be six or seven embryos in one horn of the uterus. Each blastocyst grows out as far as it can in both directions, and so comes in contact with its neighbours. I have never found them fused within the uterus, although lying in contact. I have, however, found the lower ends of the lowest embryos on each side which projected into the vagina apparently fused on one occasion. I did not examine them closely, and so cannot say whether it was a real fusion or not.

The specimen described in this paper affords no evidence in itself of the cause of the division. Whether the cause lies in the retention of an excess of germ plasma by failure of the extrusion of a polar body, as suggested by Windle (13);—or whether by the occurrence of polyspermy; or whether by the presence of two germinal vesicles in one ovum, Dareste (8), Duval (9);—or whether, in accordance with Cleland's remarks, "There can be nothing more certain than that the mass of corpuscles destined normally to form a single embryo may, under some abnormal influence, break up into two, each of which inherits all the potentialities of the undivided mass,"—we cannot judge from the specimen itself (7, p. 9).

But it is worth while to notice, by an examination of the formation of the blastocyst of the sheep, how this fission may possibly take place through what may almost be termed an accident.

The ovum of the sheep is large. At one time the embryo is a morula. The cavity of the blastodermic vesicle arises some-

what irregularly among the cells of this morula. Several cavities may appear at once (*vide* fig. 6), which normally become confluent, and result in the formation of a blastodermic vesicle, with a wall one cell thick except at one point. In some specimens strands of protoplasm are to be seen crossing this cavity. In the specimen, a section of which is represented by fig. 6, there are two cavities, C B L, C B L', which are quite separate.

Is it not conceivable that such an irregular splitting may sometimes arise in such a way that the embryonic mass becomes divided into two portions?

If this be a possible origin, we should expect to find monstrosities less frequent in such animals as rabbits or moles, where the blastocyst cavity arises as a much clearer and more regular slit than in the sheep or even pig where it is so irregular.

It seems to me that we have here indicated a very possible cause of the occurrence of twins and monstrosities in addition to those mentioned above. According to an hypothesis on the homology of the trophoblast which I have suggested in another paper (1), the epiblast and hypoblast are already differentiated in the sheep in the morula stage. Hence no embryo would be formed as a result of fission during the process of formation of the blastocyst cavity, unless cells of each kind were distributed in their proper positions in each half. It may be urged that even then such an accidental origin of a partial or complete fission of the embryo is only tenable on a very epigenetic view of development.

It is, of course, obvious that only a fission which occurred sagittally could produce twins or double monsters. A transverse fission which separated the primary and secondary centres of growth of the embryo, which presumably already exist, from each other, would hardly produce an embryo with even a possible chance of existence; for, except by a process of regeneration, neither part would acquire the organs essential to its development.

In the specimen described above, fission had occurred long before the appearance of the primitive streak, and had therefore taken place very much sooner than in any of the cases in birds recorded hitherto, with the exception of those cases in

- a-b. Line of section of fig. 2.
- CBL. Cavity of the blastocyst.
- E. Epiblastic knob of embryonic mass.
- H. Hypoblast layer of germinal area.
- H A. Hypoblast layer of the less advanced germinal area.
- H B. Hypoblast layer of the more advanced germinal area.
- S. Spermatozoa imbedded in zona radiata.
- T. Trophoblast, or main wall of the blastocyst.
- Z. Zona radiata.
- X. Point where the trophoblast has ruptured.

Fig. 1. A surface view of a specimen of a twin blastodermic vesicle of the sheep; aged 7 days. The two germinal areas are shown at A and B.

Fig. 2. A drawing of a section of the specimen shown in fig. 1, taken along the line a-b. The section passes through the edges only of the two germinal areas. The small figures A and B are more median sections of the two areas, drawn to the same scale.

Fig. 3. An enlarged drawing of a nearly median section of the embryonic area A.

Fig. 4. An enlarged drawing of a nearly median section of the embryonic area B.

Fig. 5. An outline drawing of a median section of a normal embryonic area of the sheep, of a stage corresponding to that of A.

Fig. 6. An outline drawing of a section of a young specimen of the sheep embryo during the conversion of the morula into the blastodermic vesicle.

F

x

A

a

Fig. 4

x 600

b

E

T

Z

x 600

Fig. 2

x 140

A

HA

HB

Fig. 5
 X 600

T

T

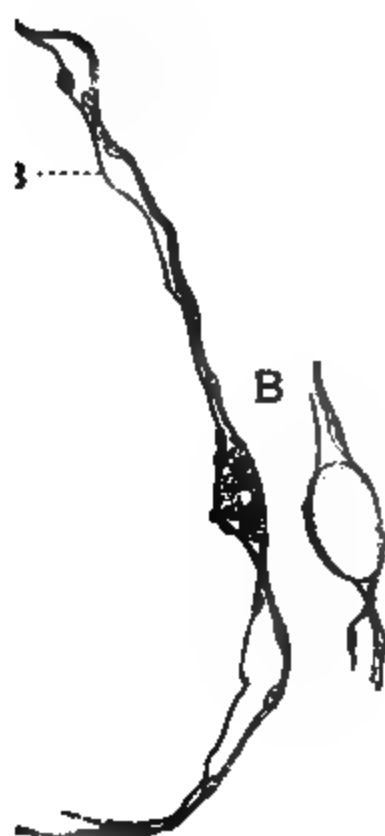
E---

---T

-T

Fig. 6
 X 600

Z



C.BL'

-C.BL

F
x
A
a

Fig. 4
x 600

B
b

I

T

Z
x 600

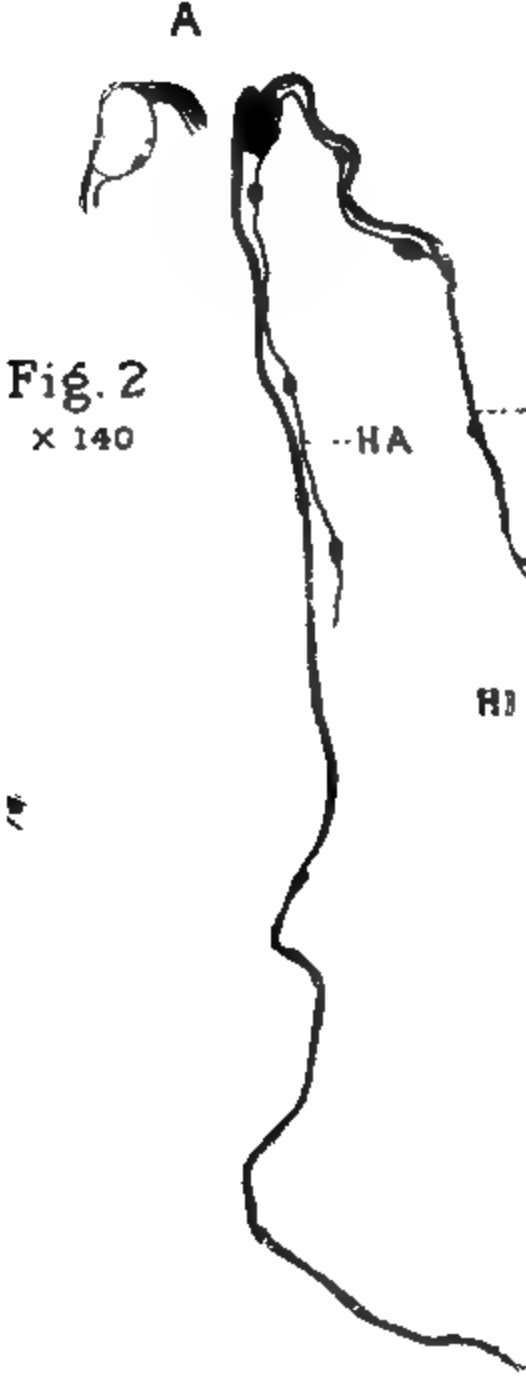


Fig. 2
x 140

Fig. 5
x 600

T-

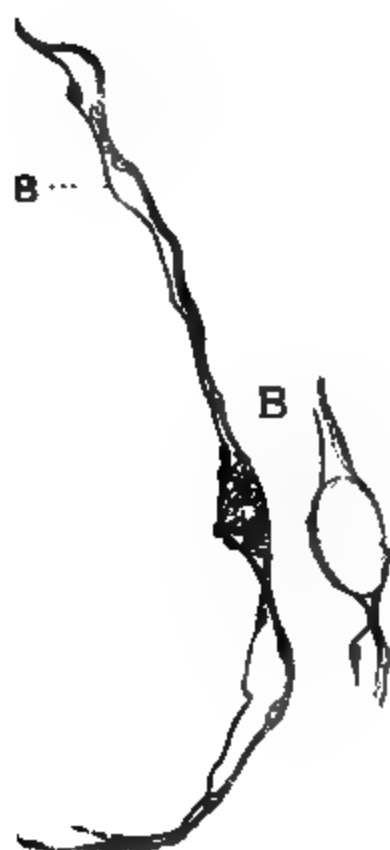
T...

E ...

... T

..T

Fig. 6
x 600



z

C.BL'--

C.BL

MODERATOR BAND IN LEFT VENTRICLE AND TRICUSPID LEFT AURICULO-VENTRICULAR VALVE.
By Professor Sir W. TURNER, F.R.S.

LEFT MODERATOR BAND.

ON two previous occasions I have communicated to this *Journal* notes on the occurrence of a moderator band in the left ventricle of the human heart.¹ I have now before me a third specimen from an adult male subject, which I employed during the present winter to illustrate my lectures on the vascular system.

The *left ventricle* was opened into by cutting through the wall parallel to and immediately to the left of the anterior interventricular groove, and not by the customary method of transfixing, which is so apt to injure some of the intraventricular structures. A strong rounded band, 27 mm. long by 5 mm. in width, was seen to pass across the ventricular cavity. It was attached by one end to the septal wall, 18 mm. from its anterior border, and by the other to the opposite wall, with the muscular fibres of which it was continuous. It lay almost transversely to the long axis of the ventricle: its lower border was 28 mm. above the apex of the cavity, and its upper border was 12 mm. below the basal attachment to the ventricular wall of the more anterior of the two papillary muscles. It consisted of muscular tissue, surrounded by endocardium.

A fibrous thread, about equal in thickness to a chorda tendinea, was attached to the ventricular wall, about midway between the base of the more anterior papillary muscle and the level of the upper border of the moderator band. It passed backwards to become connected with the posterior wall of the ventricle, close to the base of the more posterior papillary muscle, and was quite free between its two ends.

¹ Vol. xxvii., *Proceedings of Anatomical Society*, Feb. 1893, p. xix, and vol. xxx. p. 568, 1896.

The septal wall of the ventricle, as in the heart which I described in 1896, possessed, from the place of attachment of the moderator band up to the aortic vestibule, a smooth surface, almost unbroken by projecting carneæ columnæ.

The *right ventricle* was opened into by an incision along the right border of the heart, and another immediately below and parallel to the right auriculo-ventricular groove. A strong papillary muscle arose from the anterior wall. Its base extended for 20 mm. as far as the anterior edge of the interventricular septum. Immediately above, but separated by a pouch-like recess, was the moderator band of the right ventricle, which arose by three muscular bundles, two of which were continuous with the septum near its anterior border, whilst the third was connected with the anterior wall of the ventricle, not far from the septum. The right moderator band blended with the anterior papillary muscle a short distance above its basal attachment. Its maximum length was 14 mm.

When the right and left moderator bands in this heart were compared with each other, it was seen that the left was longer and thicker than the right, and was more freely differentiated from the ventricular wall. In both cavities they were muscular, so that, in considering their function, they ought not to be regarded as bands which passively moderate or restrict the distension of the chambers in which they lie, but rather as actively participating in the work of the ventricle, and by their contraction drawing the opposite walls together and assisting in the expulsion of the blood.

In its thickness and the degree of its muscularity, the left moderator band in this heart contrasted in a marked manner with those seen in the two hearts previously described. In them the bands, though longer, were much more slender, and, though muscular at the attached ends, contained in their length apparently only a single fasciculus of muscular fibre.

TRICUSPID LEFT AURICULO-VENTRICULAR VALVE.

During the present winter session the dissectors of a thorax called my attention to the *left ventricle* of a heart in which three strong muscoli papillares projected from the wall into the

cavity. They were almost equal in length and thickness, and for descriptive purposes may be named A. B. and C. A. sprang from the posterior wall, close to the left border of the ventricle; B. from the same wall, close to the right and posterior border of the septum; C. from the septum in front of and to the left of B. Each muscle gave origin in the usual way to chordæ tendineæ. As three muscles of almost equal magnitude were present, I was naturally led to examine the auriculo-ventricular opening, to see if there were not three cusps to the valve, which was found to be the case.

The largest cusp was placed obliquely in front of the opening, and was opposite the interval between papillary muscles A. and C., from each of which it received chordæ tendineæ. This cusp was also in relation to the aortic vestibule and opening; it was smooth on both surfaces, and obviously represented the normal anterior cusp of the mitral valve. The second cusp was situated opposite the interval between A. and B., from both of which it received chordæ tendineæ; it was distinctly smaller than the anterior cusp, and was situated behind and somewhat to the left of the opening. The third cusp was between B. and C., and received chordæ tendineæ from both; it was about the same size as the second cusp, and was on the right posterior part of the opening. From their smaller size, the two posterior cusps together represented the posterior cusp of the normal valve.

The cusps were all thickened, contracted, and somewhat calcified from disease, and they consequently did not present such broad surfaces as in a healthy valve.

The increase in the number of cusps in the mitral valve is an interesting variation in relation to comparative anatomy. Though in most mammals the normal number of cusps at the left auriculo-ventricular orifice is two, as in the human mitral, a larger number is sometimes seen. In the horse, for example, an accessory cusp is occasionally seen on the right of the opening. In the Cetacea, the ziphioid *Mesoplodon bidens* (Sowerby's whale),¹ though possessing two large cusps in the valve, had two distinct smaller cusps intermediate to the larger, so that the valve was definitely quadricuspidate. In a specimen of the Whale-

¹ *Jour. of Anat. and Phys.*, vol. xx. p. 164, 1886.

bone whale, *Balænoptera rostrata*,¹ the quadricuspidate division was more strongly marked, and, in addition, I found three thick stunted papillary muscles opposite the intervals between three of the cusps, whilst the fourth interval, instead of a single thick muscle, had several smaller elongated papillæ, from which the chordæ tendineæ arose. I may also state that in this heart four strong muscular moderator bands passed across the left ventricle from the septal to the ventral wall.

¹ *Proc. Roy. Soc. Edin.*, Feb. 15, 1892, p. 62.

SPONTANEOUS CURE AND TORSION OF ANEURISM IN A SHEEP. By GORDON SHARP, M.D. Edin.

THE specimen I am about to describe was found lying loose in the belly of a healthy sheep, quite close to the gall-bladder. No point could be detected as showing its former attachments. In size it was of the dimensions of a dried prune, and of almost the same colour, and it had a smooth outer covering. On carefully handling and examining, it gave the impression of having semi-solid contents. The shape was oval, and at one end there were the remains of a short pedicle, and this pedicle looked as if it had been removed by slow torsion. The general impression left on one's mind after such a preliminary examination was that the specimen was a bag containing bile in a semisolid state.

Naked-eye and Microscopic Characters.

(1) *Of the Contents.*—On slitting the sac open, a soft, semi-solid chocolate-coloured mass was seen loosely adhering to the walls. A small portion of this material was tested for bile-acids and bile-salts, but no reaction was obtained. Another portion was next tested with solutions of guaiacum resin and ozonic ether, and a blue colour was at once struck. A third portion was now diluted with normal saline solution, and examined by the low and high powers of the microscope, when broken-down blood-cells and numerous disintegration crystals were seen, with here and there red cells, granular in appearance, which had not undergone complete disintegration.

(2) *Of the Sac.*—The sac was as thin as tissue-paper (although tough in texture) in most parts, but near the pedicle it was much thicker. Various portions were hardened in weak formic aldehyde solution, and sections cut and examined by the microscope after being stained with picrocarmine solution. These differed in appearance and in tissue structure. One section was

made up almost entirely of fibrous tissue. A second contained, in addition, a large proportion of elastic and muscular tissue, the fibrous tissue being to the outside, and the muscle and elastic to the inside. A third contained only a visible amount of muscle and elastic tissues, the bulk being fibrous. In no section could any epithelial layer of cells be seen.

Nature of the Specimen.

Putting the various circumstances of structure of sac and characters of contents together, one concludes that this blood tumour was an aneurism growing from the side of one of the larger blood-vessels. We can imagine slight damage to the wall of a blood-vessel: a bulging forms, and grows steadily and slowly till it has assumed the appearance and shape of a distinct body. Instead of this swelling extending till the walls become thinned to the point of giving way, Nature has all the while been carrying on her compensatory work. Damage and compensation have been proceeding side by side, but compensation has been in excess of damage. The contents of the sac act as a compensatory agent, by disintegrating more and more as they are removed from the blood stream, till finally the sac and contents becomes a body foreign to the vessel from which it had its origin. Time completes the work, and the aneurismal swelling drops off.

Practical Deductions.

Aneurism is more curable than on first consideration we are led to think, for it is a common experience to find remains of aneurisms in the dead body. Excluding the region of the brain, if the aneurism occurs on one of the vessels at a distance from the heart, the condition is most likely due to an accident, and Nature may be able to complete a cure. In aneurisms of this class, one may reasonably hope for success crowning our efforts if we follow the methods employed by Nature. We may remove the tumour, or employ means to promote solidification of the contents of the sac. But when the aneurism occurs on the vessels of the brain, or on the vessels close to the heart, then there is more likelihood of the condition being dependent on a

general disease of the blood and of its vessels, and for this reason we have to place aneurisms of these parts in the category of maladies highly incurable. We may try iodide of potassium, which often produces marked benefit, and may even remove the morbid growth. Here the drug acts not in virtue of its depressant effect on the circulation, as is sometimes supposed, for even with very large doses this effect is almost inappreciable. Its action is that of an eliminant, removing the morbid deposits due to syphilis, gout, rheumatism, or other poison; and so Nature is placed under circumstances the most favourable to effect a cure.

CONCERNING THE PARATHYROID GLANDS: A
CRITICAL, ANATOMICAL, AND EXPERIMENTAL
STUDY. By D. A. WELSH, M.A., M.D., *Assistant to the
Professor of Pathology in the University of Edinburgh.*
(PLATE VII.)

(Continued from page 307.)

PART II.—ANATOMY.

FOR the purposes of this study, the parathyroid glands were investigated in more than forty cases in man, from earliest infancy to advanced age, including the human foetus at six months; and, among other mammalia, in the ox, in the sheep, both adult and foetal, in the rabbit, in the cat, and in the ferret. It is not intended, however, that the following description should apply to all these cases, but that it should be almost exclusively limited to the anatomy of these glands in the human subject. The other animals will be referred to only in so far as they illustrate conditions analogous to those which occur in man.

In dissecting the parathyroid glands in man, one is at first confused by the number of separate nodular bodies which lie in more or less close proximity to the thyroid, and which are, especially at first, liable to be mistaken for them. Among such bodies may be noted accessory thyroid glands, nodules of thymus tissue, masses of lymphadenoid tissue, hæmolymp glands, carotid glands, and nodules of adipose tissue. It is at first impossible to distinguish with certainty by the naked eye between these structures and the parathyroid glands, and I was therefore obliged at the outset to examine histologically a large number of tissues from each case. By this somewhat tedious process, I was gradually enabled to identify the parathyroids with greater certainty, and it soon became apparent not only that they were very constant in their occurrence, but that they occupied fairly definite positions, so that the investigation of subsequent cases

was greatly facilitated. As will be shown later, their histological features are so striking and so characteristic that little difficulty is ever experienced in identifying them under the microscope.

General Characters.

Number.—It may be stated as a general rule that in man there are in all four parathyroid glands—two on each side. Cases in which apparently there are fewer may be explained on several grounds, two of which may be here noted: (1) an abnormal distribution of the glands, so that one or more has escaped observation; and (2) a more or less intimate connexion between two of the glands, so that they appear externally as one mass. That they may occasionally occupy widely different positions will be shown later when their usual sites and relations are described, and it is therefore not unreasonable to suppose that in the small minority of cases in which they cannot all be found, the missing gland has probably been overlooked. But it may sometimes also happen that a gland is missing on one side because it has become bound up in the same capsule either with the other gland of the same side or with the corresponding gland of the opposite side. Sometimes this connexion is not at all close, as in one case where the two superior parathyroids were found on the same side with their capsules united by a strand of dense fibrous tissue about 10 mm. long. More often the union is closer, so that the two glands appear to form a single body; but, even in this case, microscopic examination shows that the two organs, although enclosed in the same capsule, are completely separated by a fibrous septum. A remarkable instance occurred in one child examined, in which no parathyroids could be detected on the right side after the most careful search, whereas two were readily found on the left. Under the microscope, however, it appeared that each of the two left parathyroids was in reality double, and contained two separate organs within the same capsule.

Size and Shape.—In size they show considerable variety. Most commonly they measure about 6 or 7 mm. in length, about 3 or 4 mm. in breadth, and about 1.5 or 2 mm. in thickness. In one of the largest examined the length was 15 mm., the

breadth 6 mm., and the thickness 3 mm. The length is the most variable dimension: it is not at all uncommon to find them 10 or 11 mm. long, while the breadth and thickness remain of average measurement. The most constant dimension is the thickness: it is somewhat exceptional to meet them more than 2 mm. thick, or less than 1.5 mm.

In shape they present one of two forms. (1) In the majority of cases they are oval, and only rarely approximate to a circular outline. With few exceptions they are very thin, forming flat ovoid plates or discs, which are moulded to the form of the subjacent structures. (2) It not infrequently happens that one extremity is tapered off to a fine point, so that they have a flattened pyriform outline. When this occurs the gland is connected by a distinct stalk or process with the thyroid itself. Along this stalk the parathyroid tissue passes for some distance, but usually ceases before it reaches the thyroid. The vessels that supply the parathyroid are also carried by this process, and enter or leave the gland by its tapering extremity. This form is very typically seen in the ox, in which it is the most common condition.

In the child they present the same general form as in the adult, but they appear to be relatively much larger, though I have not yet examined a sufficient number of cases in children to enable me to make a definite statement. In a child nine months old, for example, the two left parathyroids measured 3 mm. by 2 mm. by 1 mm., and 4 mm. by 2 mm. by 1 mm. respectively.

Weight.—The average weight of the fresh parathyroid in the adult is about 0.035 grammes, but the limits of variation are very wide, extending from a minimum of 0.010 grammes to a maximum of 0.100 grammes, or even more. I have not been able to establish any relation between the weight of the parathyroids and that of the thyroid. Relatively large parathyroids may be associated with small or with large thyroids, and the same statement applies to relatively small parathyroids. The same indeterminateness characterises their relation to the pituitary also.

Colour.—In colour they present, as a rule, a distinct contrast to the thyroid. Their characteristic hue is yellow, with varying

admixtures of red and brown. The yellow tint is due to the infiltration of fat cells in clusters between the masses of epithelial cells of the gland,—a condition which appears to be normal when present to a slight extent, but which may be met in an extreme degree.

Surface.—The surface is uniformly soft and smooth, much smoother than that of the thyroid, and usually shows a well-marked delicate reticulum of minute veins just underneath the capsule. The light yellowish colour and the remarkably smooth surface with its fine venous reticulum are appearances which materially aid the identification of the parathyroids by the naked eye.

Position and Relations.

The two parathyroid glands on each side have a very constant position relatively to each other. One of them is almost invariably situated above and behind the other, and they may therefore be distinguished as the 'posterior superior' and the 'anterior inferior' parathyroid respectively. It will be convenient to describe the relations of each separately.

I. *The posterior superior parathyroid* of each side is much more constant in its position, and much more easily found than the anterior inferior glandule. Briefly, it may, as a rule, be said to lie on the posterior wall of the œsophagus or pharynx, at the level of the lower edge of the cricoid cartilage, immediately internal to the posterior margin of the lateral thyroid lobe, and in front of the prevertebral division of the cervical fascia. It usually has very definite relations to most of the following structures:—(1) the thyroid gland, (2) the œsophagus or pharynx, (3) the prevertebral fascia, (4) the inferior thyroid artery, (5) the recurrent laryngeal nerve, (6) the lateral thyroid ligament. It may, in addition, have quite peculiar relations to (8) accessory thyroid glands and (9) nodules of adipose tissue. In illustration of these points a series of outline sketches has been prepared by Mr Richard Muir. The sketches are reduced from outlines drawn to scale from actual dissections, and are shown in fig. 2.

(1) Perhaps the most important relation consists in the fact

that the parathyroid is quite separate from the thyroid tissue. In the great majority of cases it lies entirely outside the thyroid capsule. In a few cases, however, it is found enclosed within the same capsule, but what really happens is that the thyroid capsule splits to enclose the parathyroid. In my experience the tissue of the parathyroid is never directly continuous with that of the thyroid, but always separated from it by a distinct septum of fibrous tissue. The parathyroid may even occupy a shallow depression on the outer thyroid surface, but it is never enclosed within the thyroid substance to any appreciable extent.

While the commonest position of the parathyroid relatively to the thyroid is immediately internal to the posterior margin of the lateral lobe, it may show considerable variations. Thus it may not be found until the posterior thyroid margin has been reflected outwards, and then it lies underneath or internal to the inner (tracheal) surface of the lateral lobe (fig. 2, *b*); more rarely it is found on the external surface (fig. 2, *c*), and still more rarely at any considerable distance from the posterior edge (fig 2, *e*).

(2) Its relation to the œsophagus and pharynx is simple and very constant. It is almost invariably found on the posterior wall at or near the junction between the two. The long axis of the parathyroid is usually parallel to that of the œsophagus or pharynx, and its flattened surface is closely applied and moulded to the muscular wall.

(3) Its relation to the prevertebral fascia is most important, and is diagrammatically represented in Pl. VI. fig. 1, *b*. It invariably lies in front of the fascia, and is therefore partitioned off in the same compartment with the thyroid, trachea, and œsophagus.

On this relation depends a practical method by which these parathyroids may most readily be secured. The thyroid should not be dissected off from adjacent structures, but should be removed along with the larynx and trachea and the pharynx and œsophagus, so that their mutual relations remain undisturbed. The posterior aspect of this mass of tissue should then be examined, when, on stretching or incising the layer of fascia where the posterior margin of the thyroid meets the œsophagus, the posterior parathyroid is usually at once revealed. Care

should be taken that the trachea and oesophagus are divided at as low a level as possible, otherwise, as will appear later, the anterior parathyroids may escape observation.

(4) It may be stated as a general rule that the centre of the posterior parathyroid is situated about the level of the lower edge of the cricoid cartilage, but it is seldom exactly so placed. More commonly it is a few millimetres higher or lower, and very rarely is there absolute symmetry on the two sides.

In exceptional cases it may be placed very high, so that it lies on the inferior cornu of the thyroid cartilage, as in fig. 2, *c*, or it may be found as low as the sixth tracheal ring, as in fig. 2, *e*. The latter is a very exceptional position, but it explains how, if the trachea had been cut short, even the posterior parathyroid of that side would not have been detected.

(5) *and* (6) The inferior thyroid artery and the recurrent laryngeal nerve pass upwards in front of the posterior parathyroid; and where the gland occupies its usual position, they are also internal to it. This relation marks one of the distinctions between the posterior and the anterior parathyroids, for the latter always lie in front of the artery and nerve.

(7) The lateral thyroid ligament forms an important relation when the posterior parathyroid is overlapped by the lateral thyroid lobe. In such cases the parathyroid is never found in front of the ligament, but invariably behind and external to it, often actually lying on its posterior surface (*cf.* fig. 1 and fig 2, *b*). This ligament is very constantly present, and passes from the tracheal surface of the lateral lobe, about an inch in front of its posterior margin, upwards, backwards, and inwards, to be attached to the lower edge of the cricoid cartilage and the first ring of the trachea.

(8) There is sometimes an interesting relation between the parathyroid and accessory thyroid glands. By the latter term is understood detached nodules of thyroid tissue, which retain all the morphological characters, and probably also share in the function of the main gland. One of the positions in which they are comparatively common is in the region of the posterior parathyroid, and it occasionally happens that both the accessory thyroid and the parathyroid are enclosed in the same capsule, but in every such case the different glandular tissues are com-

pletely separated by a distinct fibrous septum. There is never any continuity of tissue, nor any evidence of the transformation of parathyroid into accessory thyroid tissue.

An intermediate condition is sometimes met where a piece of thyroid tissue is only partially detached from the main gland and remains continuous with its posterior margin by a narrow isthmus. The parathyroid may then be included in the capsule of the projecting mass of thyroid tissue, but is never continuous with it.

(9) Lobules of adipose tissue are often intimately related to the parathyroids; for not only are they frequently encapsuled together, but islets of fat cells are very commonly found between the masses of epithelial cells in the gland itself. In every case, however, the gland tissue is partitioned off by a secondary capsule of its own within the common fibrous envelope. The fact that the parathyroid may be thus bound up with a lobule of adipose tissue, and the fact that, owing to the infiltration of the gland with fat cells, its colour may be distinctly yellowish, often make its recognition a matter of extreme difficulty, and so add another to the many reasons why it should sometimes elude observation.

II. *The anterior inferior parathyroids* have a much more inconstant position and more indefinite relations. They are accordingly more easily overlooked than the corresponding superior pair. In the majority of cases, however, they occur in one or other of two positions, which may be roughly distinguished relatively to the thyroid and trachea, as (1) postero-lateral and (2) antero-lateral. Although within the limits of these positions considerable variations are met, yet there is always a certain rude symmetry in their arrangement, for they are usually either both postero-lateral or both antero-lateral, so that either both are found on dissecting the thyroid and trachea from behind, or both are found in front. A reference to the outline drawings illustrative of their positions will make this clear (*cf.* fig. 2, *a*, *b*, *d*, and *f*).

(1) When they occupy the postero-lateral position, they are found either closely applied to the thyroid or at a variable distance below it. (*a*) In the former case they are usually applied to the lower edge of the lateral thyroid lobe just in front of its junction with the posterior margin, and frequently

slightly overlapped by it. In this position they come into relation with the inferior thyroid artery, on the first thyroid branch of which they usually rest. They lie thus in front of the artery and recurrent laryngeal nerve, and are separated by these structures from the posterior superior parathyroids. Having their flat surface in close apposition to the inferior thyroid margin, they often lie obliquely with their long axis running from above downwards, forwards, and outwards. From the trachea they are separated only by areolar and fatty tissue, and are placed on the postero-lateral aspect of the third or fourth ring. They do not, as a rule, in this position come into direct relation with the œsophagus. (*b*) In the latter case they may be placed immediately below the thyroid, and sometimes dependent from it by a short stalk, or they may occur at considerable distances from it, and entirely unconnected with it. In exceptional instances they are found as low as the eighth tracheal ring, and may come into relation with the side of the œsophagus (*vide* fig. 2, *a* and *b*).

(2) When they occupy the antero-lateral position, they are usually placed at some distance below the thyroid; more rarely are they closely applied to its lower margin. They are often found in the immediate proximity of one of the inferior thyroid veins, and imbedded along with other glandular bodies in a small mass of areolar and adipose tissue on the front of the side of the trachea. They may occur at widely different levels, and sometimes as low as the tenth tracheal ring. Their long axis lies more often oblique than parallel to that of the trachea (*cf.* fig. 2, *d* and *f*).

Vascular Supply.

The vascular supply of the parathyroids was investigated (1) by ordinary dissection; (2) by microscopic examination of transverse and longitudinal sections of the glands; (3) by injection of the inferior thyroid artery in the adult, and of the aorta in the human foetus. As a result of these various methods, the following conclusions were reached:—

The arterial blood is supplied directly or indirectly by the inferior thyroid artery. This is invariably the case with the posterior superior parathyroid, and nearly always the case with

the anterior inferior gland also. When the latter occupies an aberrant position, however, it appears to derive its blood supply indifferently from the nearest arterial source. By ordinary dissection, a small twig from one of the thyroid branches of the inferior thyroid artery can usually be traced into the parathyroid; and by injection of the inferior thyroid artery on one side, the parathyroids of that side, along with adjacent portions

No. 1.—Transverse section of human parathyroid to show the central artery and vein, and also islets of adipose tissue along the course of the primary vascular branches. $\times 50$ diam.

of the thyroid, and the corresponding halves of the trachea, cesophagus, etc., will also be injected.

Only one artery, as a rule, enters each parathyroid, usually at its more tapering extremity. It then runs parallel to the long axis of the gland, and, on transverse section, is found to occupy a more or less central position. From the central artery lateral branches are given off at frequent intervals along its course. They do not pass off at right angles to it, but radiate obliquely, being directed towards the broader extremity of the gland. Hence, in transverse sections, they too are cut somewhat transversely; their course is best seen in longitudinal sections of the gland.

The venous return is effected in two ways: (1) By venous branches accompanying the arteries, and opening into a central channel, which runs alongside the central artery, and emerges with it. The veins into which these vessels discharge vary according to the position of the parathyroid. Thus, they may communicate with adjacent thyroid veins, or they may join the venous branches on the surface of the thyroid. (2) Numerous venous channels lie immediately underneath the capsule of the parathyroid, and form the delicate reticulum, which is a character of the naked-eye appearance of the gland. Microscopically, they may appear as dilated, thin-walled sinuses. They do not seem to have any constant course, but empty into œsophageal, tracheal, or thyroidal veins indifferently.

Histology.

The minute anatomy of the human parathyroid presents many remarkable features, some of which have never previously been put on record. The tissues examined were all taken from the post-mortem room; and though an endeavour was made to fix them in as fresh a condition as possible, yet the possibility of post-mortem changes must always be kept in view. Hence, minute histological details will not be discussed, and only a brief account will be given of some of the more salient points in the structure and disposition of the gland cells.

The parathyroids are essentially epithelial structures, which in some respects bear a close resemblance to other epithelial organs, such, for example, as the adrenal, the anterior pituitary lobe, and the embryonic thyroid, but which are, on the whole, strikingly and characteristically different. The epithelial cells of which they are composed may belong to one or other of two distinct varieties. I. Cells which have a relatively small and clear protoplasmic body, and a relatively large and clear nucleus. These cells constitute the greater part of the gland tissue, and are constantly present in every case. For convenience they will be referred to as the 'principal cells.' II. Cells which have a relatively large and usually granular protoplasmic body, and a relatively small and dark nucleus. They occur in a very large proportion of cases, though not in all, and are never so

abundantly present as the former variety. As the granules of the cell protoplasm are highly oxyphile, these cells will be designated the 'oxyphile cells.'

I. *The Principal Cells*.—Although they conform to the brief description given above, they may show considerable variation both in the details of their structure and, more particularly, in their arrangement within the gland.

In their structure the chief variations occur in the size and shape of the individual cells, in the intensity of staining of the cell protoplasm, in the size and shape of the nucleus, and in the disposition of its chromatin. These differences are usually correlated with differences in the arrangement of the cells, and will be noted along with the description of the latter. The cell protoplasm may appear absolutely clear and hyaline, but more frequently it takes up a diffuse stain of varying degrees of intensity. It may be stated, however, that no matter how deeply the cell protoplasm may stain, there is almost never any distinct granularity, and that, in the exceptional instances in which it is present, the granules are exceedingly fine, and take only basic dyes. The nucleus is usually ovoid, and shows a distinct nuclear membrane and intra-nuclear network; it is in many cases very similar to that of the epithelial cells of the thyroid.

In regard to their arrangement, at least four types may be noted according to which they may be disposed. It is comparatively rare, however, to find a parathyroid whose cells have only one type of arrangement throughout. It much more commonly happens that several different types coexist in the same gland.

Type (1).—The principal cells may form a uniform mass, practically continuous in every direction. Throughout considerable areas of such a mass, no intercellular stroma can be detected, and the cell walls are everywhere in direct apposition. The cell outlines are irregularly polyhedral, but contiguous cells vary greatly in size and shape. At infrequent intervals the continuity of the mass is interrupted by delicate strands of cellular connective tissue, carrying a small blood-vessel or capillary, but, on the whole, this arrangement is characterised by a very slight degree of vascularity. It is when the principal

cells have this disposition that the cell protoplasm is most frequently hyaline or most faintly stained. In some cases, indeed, the protoplasm does not take on any appreciable stain, and the cell appears to consist merely of a cell envelope and a nucleus, which is often eccentrically placed.

Type (2).—The cells may be arranged in the form of masses, which, though continuous in every direction throughout small areas, show a greater tendency to become broken up into

No. 2.—Human parathyroid, showing uniform continuous arrangement of the principal cells, and their clear cell protoplasm. (Type 1.) $\times 200$ diam.

anastomosing columns or cell trabeculae, between which are found capillaries and small blood-vessels in a fine connective-tissue stroma. This disposition represents a stage in the subdivision of the epithelial elements more advanced than in the first type. The cell protoplasm is somewhat more deeply stained, the cell outlines usually more rounded, and the whole cell apparently smaller than in the preceding.

Type (3).—The cells may form distinct branching columns, sometimes thick, sometimes slender, which on section appear as discrete masses, closely resembling the solid masses of epithelial cells in some forms of cancer. This type is to be regarded as

a still more advanced stage of subdivision. Between these isolated masses of cells may be found either a delicate capillary reticulum with an exceedingly fine fibrillar stroma, or processes of denser fibrous tissue carrying larger vessels. The larger cell masses may be irregularly subdivided by the penetration of capillaries from the margin between the epithelial cells. As a rule, the cells are fairly large, and have a clear, faintly-staining protoplasm. At the periphery of the masses the cells are often

No. 3.—Section of human parathyroid, showing the principal cells arranged in discrete masses separated by a fine capillary reticulum. (Type 3.)
× 200 diam.

smaller, and their protoplasm more deeply stained than in the centre.

Type (4).—The principal cells may form definite acini, so that the structure resembles secreting gland tissue. This is the most advanced stage of specialisation acquired. The cells are grouped in a single layer round a small circular, central lumen. Adjacent acini are often placed in such direct contact that only the contiguous cell-walls mark the boundary between them. More commonly they are separated by vascular septa of connective tissue. The epithelial cells are usually large and

columnar, or at least irregularly elongated. The protoplasm stains very variously, being sometimes exceedingly clear and faint, at other times darker with very fine basiphile granulations. Differences of staining may occur in cells lying side by side in the same acinus. The nuclei, as a rule, occupy the extremity of the cell directed to the lumen, but they may be central or peripheral. The central lumen may, although rarely, be entirely free; more usually it is occupied by a small globular mass; whose

No. 4.—Section of human parathyroid, showing acini containing colloid, and lined by the principal cells (Type 4), and illustrating resemblance to the anterior pituitary lobe. $\times 200$ diam.

micro-chemical reactions show that it consists of a colloidal substance. In exceptional cases the colloid forms a relatively large mass, which distends the lumen and causes the epithelial cells to acquire a low columnar or cubical shape. It is very unusual to find more than a small part of the gland showing this acinous arrangement, but it is exceedingly common in small areas.

II. *The Oxyphile Cells.*—The oxyphile cells have a very characteristic and constant structure. The cell body is, on the whole, larger than the principal cells, and its protoplasm shows

a distinct fine granulation. The granules are highly oxyphile, and readily take up eosine and other acid dyes. They show a striking resemblance to the granules in the erythrophile cells of the pituitary body, which are also highly eosinophilic. Sometimes a fine vacuolation of the cell protoplasm is also met with. The nucleus is both relatively and absolutely smaller than the nucleus of the hyaline cell. In outline it is more nearly circular. Its chromatin is more densely arranged, so that no nuclear net-

No. 5.—Human parathyroid, showing compact mass of granular oxyphile cells beneath the capsule. (Type 1.) Contrast with adjacent mass of principal cells. $\times 200$ diam.

work can be detected, and the entire nuclear mass appears uniformly and darkly stained.

In their arrangement they may show four different types, but, unlike the principal cells, their structure remains practically constant throughout.

Type (1). The cells form a uniform mass continuous in all directions and only very exceptionally interrupted at any part by connective tissue or capillaries. Such masses may occur in small islets scattered irregularly throughout the gland tissue. Very commonly they are found immediately beneath the capsule,

forming a somewhat wedge-shaped area, whose broad end abuts on the capsule. Where they are not in contact with the capsule, the cells forming the margins of these islets are directly continuous with the adjacent principal cells, but they tend to preserve an uninterrupted and abrupt line of demarcation, and seldom become mixed with the other cells.

Type (2).—The cells tend to be arranged in continuous anastomosing columns, between which connective tissue septa

No. 8.—Human parathyroid, showing several different arrangements of the oxyphile cells, and vacuolation of their protoplasm. $\times 200$ diam.

and capillary channels are found. The columns do not, as a rule, terminate abruptly, but first include a few of the principal cells in their course, then appear only as scattered granular cells among the others, and finally cease.

Type (3).—The granular cells occur irregularly scattered among the principal cells, either singly or in groups of three or four, without definite arrangement. They simply form constituent elements of the formation adopted by the principal cells among which they lie. This condition occurs not uncommonly in glands which show no other sign of the presence of oxyphile cells.

Type (4).—The cells may form definite acini, the lumen being

occupied by a mass of colloid material. As compared with the corresponding arrangement of the principal cells, however, this is a very exceptional condition.

As already mentioned, the granular oxyphile cells may not be present at all; and even when they do occur, they never constitute more than a small proportion of the total epithelial tissue.

The Capsule and Connective Tissue.—The parathyroid is invariably completely invested by a capsule of fully formed fibrous tissue. Frequently the parathyroid is included in the same fibrous envelope along with a lobule of adipose tissue, an accessory thyroid gland, or the thyroid itself. In such cases, however, the fibrous lamellæ of the larger envelope split at the margin of the parathyroid and enclose the gland between the two layers, so that its tissue is never continuous with that of any other structure. From the deep surface of the capsule fibrous septa may be given off, which penetrate the gland, and produce an irregular lobule formation. This subdivision into lobules is rarely well marked; more frequently, only rough indications of lobules are seen. It is quite independent of the type of cell arrangement. Septa of dense fibrous tissue are also found alongside the larger vessels in the gland. As the vessels become smaller, the fibrous tissue either becomes more cellular, or is replaced by delicate fibrils of connective tissue. The ultimate ramifications depend upon the special arrangement of the epithelial cells, and have already been indicated. Reference has also been made to the very frequent occurrence of isolated clusters of fat cells on the course of the septa within the gland.

The Stalk or Duct-like Process of the Parathyroid.

The occasional occurrence in man of an attenuated process along which the vessels may enter and leave the parathyroid has already been noticed. In appearance it often suggests a duct, but, on examining cross-sections at various intervals, I have never been able to find any trace of such a structure, although the gland tissue may be prolonged upon it for some distance. The only histological indication of a duct in man was met in sections of a large parathyroid, in which a few large spaces were

No. 7.—Transverse section of duct-like process of parathyroid of ox,
showing the duct spaces. $\times 100$ diam.

No. 8.—Transverse section through front of neck of sheep embryo (6.5 cm.).
The lumen of the trachea is seen in the upper part of the field; that of the
oesophagus below it. The large mass of the thyroid is seen on each side,
and on the left of the field, between the thyroid and oesophagus, a parathyroid
is seen, sharply marked off from the thyroid. The corresponding structure
on the right does not appear in the section. A small nodule of thymus
tissue is seen on each side between the thyroid lobe and the carotid artery.

found lying just outside the gland tissue. These spaces were lined by cubical epithelium, and were filled with colloid matter of different degrees of density.

In the ox, however, the parathyroid has almost invariably a very distinct stalk by which it is attached to the tracheal surface of the thyroid. Along this stalk the gland tissue is prolonged for a short distance, as in the human subject; but beyond this a more definite duct-like structure can be found. The solid formation of polygonal cells becomes replaced by a series of hollow channels lined by cubical or low columnar epithelium, and often containing colloidal matter. This appearance may be seen in transverse sections of the stalk, at any point between the termination of the gland tissue proper and its junction with the thyroid. In the stalk the duct-like spaces are always multiple: even close to the thyroid they do not appear to coalesce to form a single channel. I have not been able satisfactorily to determine their mode of union with the thyroid, on account of the dense bed of fibrous tissue through which they finally pass; but the stalk can often be traced quite readily into the connective tissue between the lobules of thyroid substance.

Comparison with other Organs.

I. The anterior lobe of the pituitary body bears a close resemblance in some of its structural features to the parathyroid glands.

(1) In both there occur two kinds of cells, the one characterised by a homogeneous diffusely staining protoplasm and a relatively large pale nucleus, the other by a relatively small dark nucleus and an oxyphilic granulation of its protoplasm.

(2) In both there may occur acini, whose lumina may be occupied by small lobules of colloid substance, or, more sparsely, larger spaces containing larger masses of colloid.

II. The structure of embryonic thyroid tissue has little in common with that of the parathyroid.

(1) From the account of the adult parathyroid already given, it is obvious that the majority of the appearances there described do not correspond to any condition met in the embryonic thyroid at any stage of its development.

No. 9.—Parathyroid (injected) of human fetus (6 months), showing distribution of vascular supply ; contrast with structure of thyroid. $\times 50$.

No. 10.—Thyroid (injected) of human fetus (6 months), to show contrast with vascular arrangement and structure of parathyroid. $\times 50$.

(2) The structure of the parathyroid becomes differentiated from that of the thyroid at a very early period of development, practically as soon as the structure of the thymus is thus differentiated; and when, from this period onward, the embryonic parathyroid is compared with the embryonic thyroid of the same stage, a striking dissimilarity is apparent.

I do not consider that the tissue of the parathyroid is essentially the same as that of the thyroid, in the sense, for example, that accessory thyroids are essentially the same as the main gland. I do not even regard the parathyroid as bearing any more intimate genetic relation to the thyroid than, for example, the thymus does. Nor have I ever met any evidence that the parathyroid can morphologically develop into thyroid tissue.

I have much pleasure in recording my special indebtedness to Professor Greenfield, in whose laboratory this investigation was conducted; and in acknowledging the kindness of Dr Clouston, who permitted me to make use of specimens from the Royal Edinburgh Asylum. I have to express my thanks for opportunities for collecting material to both the Pathologists of the Royal Edinburgh Infirmary, and I have to acknowledge similar assistance from many other sources. My thanks are also very specially due to Dr W. F. Robertson, who was the first to bring the subject of the parathyroid glands under my notice; and to Mr Richard Muir for the excellent microphotographs and sketches he has prepared in illustration of this work.

EXPLANATION OF PLATE VII.

Fig. 1. Diagrammatic representation of a transverse section through the front of the neck at the level of the lower border of the cricoid cartilage, to illustrate the relations of the posterior superior parathyroids on the right to the prevertebral fascia, etc., on the left to the lateral thyroid ligament.

The lateral thyroid lobes, the trachea, œsophagus, and part of a vertebral body, are easily identified; other structures are indicated by letters.

- a. Lateral thyroid ligament.
- b. Posterior superior parathyroid.
- c. Carotid sheath.
- d. Prevertebral fascia.
- e. Recurrent laryngeal nerve.
- f. Inferior thyroid artery.

Fig. 2. Outline sketches, reduced from actual dissections, to illustrate possible positions of the parathyroids.

a and *b* represent posterior views of two different cases.

c and *d* represent the posterior and anterior views respectively in a third case.

e and *f* represent corresponding views in a fourth case.

Further description will be found in the text.

PART III.

AN EXPERIMENTAL STUDY OF THE PARATHYROID GLANDS OF THE CAT.¹

Summary of Experiments.

First Series.—Removal or destruction of all the four parathyroids without removal of the thyroid; three operations (one doubtful).

No. 1.—Acute symptoms; died within five days.

No. 2.—Very severe symptoms; died within four days.

No. 3.—(Doubtful) delayed symptoms; died within twenty-one days.

Second Series.—Removal or destruction of less than four parathyroids without removal of the thyroid; four operations.

No. 4.—Removal of three parathyroids; acute symptoms for ten days, recovery; no subsequent symptoms; killed after four months.

No. 5.—Removal of three parathyroids; no symptoms; killed after five months.

No. 6.—Removal of three parathyroids; no symptoms; killed after two months.

¹ A more detailed account of these experiments will be found in the *Journal of Pathology and Bacteriology*, 1898.

No. 7.—Destruction of two parathyroids; no symptoms; killed after five and a half months.

Third Series.—Removal of the thyroid and some of the parathyroids, the remaining parathyroids being retained; three operations.

No. 8.—Retention of one parathyroid; acute symptoms; died within six days.

No. 9.—Retention of two parathyroids; no symptoms; killed after one month.

No. 10.—Retention of two parathyroids; no symptoms; killed after three and a half months.

Fourth Series.—Removal of the thyroid and all the four parathyroids together; mouth administration of fresh ox parathyroid; two operations.

No. 11.—Severe symptoms, in spite of relatively enormous doses; died in eleven days.

No. 12.—Died of acute bronchitis in three days.

Conclusions.

1. Removal of all the four parathyroids in the cat may cause acute and severe symptoms, with a rapidly fatal issue, even though the thyroid be retained practically uninjured.

2. Removal of three parathyroids alone may not lead to death, but may cause transient symptoms, similar to those which result from removal of all the glandules; loss of two parathyroids alone may not produce any appreciable change.

3. Removal of the thyroid and some of the parathyroids may lead to death with acute symptoms if only one parathyroid is left, but may not induce any obvious derangement if two parathyroids are retained,—at least, not for several months.

4. Mouth administration of the fresh parathyroid of the ox may have no effect, either in mitigating the symptoms, or in averting death after removal of the thyroid and parathyroids together.

c *d*

Fig. 2.

b

e

f



b

f

e

b

THE CAUDAL LIMIT OF THE LUMBAR VISCERAL
EFFERENT NERVES IN MAN.¹ By N. BISHOP
HARMAN, B.A., M.B., M.R.C.S., *St John's College, Cambridge,*
Demonstrator of Anatomy, Cambridge University.

1. *The Lumbar Visceral Nerves in Lower Animals.*

THE first marked advance towards the elucidation of the arrangements and functions of the sympathetic nervous system was made in the work published by Gaskell (1) in 1888, entitled, "The structure and function of visceral nerves."

In 1842 Bidder and Volkmann (2) had made the generalisation that the sympathetic system was characterised by a predominating presence in its strands of bundles of fine medullated fibres, of very much smaller size than the large medullated fibres of the posterior roots, and therefore still smaller than the large motor fibres of the anterior roots.

There was some idea that these small medullated fibres were derived from the central nervous axis, for in 1846 Snow Beck (3) writes:—"I am convinced that the tubular fibres are derived from the spinal nerves, and not from the sympathetic chain"; but he knew nothing of the relation of white and grey fibres. Onodi (4) in 1884 showed the connections of the white fibres, and gave a general scheme of their distribution.

From amongst the many conclusions and suggestions of Gaskell's paper (1), I would here summarise three anatomical points, as being relevant to this research:—

1. That small white fibres are the essential part of the white ramus communicans.

2. That these white fibres are of characteristic small size ($1.8\ \mu$ to $2.7\ \mu$) and bundle formation.

3. That the range of the outflow from the central axis is from the 10th to the 25th spinal nerves of the dog (2nd thoracic to 2nd lumbar) inclusive.

¹ A thesis for the degree of M.B.

Gaskell also noted in the rami the presence of large medullated fibres of the size of 8 to 12 μ . On these Edgeworth (5) worked, and showed that they were not connected with the sympathetic ganglia, but that they terminated in Pacinian bodies; also that their trophic cells were probably situated in the posterior root ganglia, that is, that they were sensory fibres. Edgeworth appears to have believed the distribution of these sensory fibres was limited to the range of small white efferent fibres (10th to 25th nerves); Langley (6), however, showed that such fibres extended below the 2nd lumbar, and that other smaller white fibres of afferent function could be found scattered amongst the grey fibres.

The presence, therefore, of a few *scattered* white fibres in a ramus otherwise grey, does not constitute that ramus a white ramus.

The efferent function of the small white fibres which make up the white rami, though partially indicated by Snow Beck, Remak, and Bernard, may be considered to have been established by Gaskell (7) in his earlier work on the cardiac nerves of the tortoise. It has since been fully established by Langley, Dickenson, and Anderson, by experimental methods and with the aid of nicotine.

2. *The Lumbar Visceral Nerves in Man.*

As regards the outflow of these nerves in the human subject, our knowledge does not extend so far.

Experimental methods are, of course, impracticable; observations derived from pathological conditions are too gross to be of value. The general similarity of the arrangements of the spinal or sympathetic connections and distribution in both man and beast can be seen by the examination of the careful descriptions and drawings of the dissections of Snow Beck (3), and the later descriptions and plates of Frankenhaeuser (8), both from female subjects; with the plates by Langley and Anderson (9) illustrating their dissections of cats. Also the presence of the small medullated fibres in the anterior roots of spinal nerves in man was noted by Gaskell, and a single dissection of the lumbar rami in man by Latham is recorded by Langley (10).

With regard to the limits of the offset from the spinal nerves

of these small fibres, I have endeavoured to obtain some exact determination. The effort has been made particularly in the lumbar region.

The methods employed have been those of dissection, staining, and subsequent teasing of the stained nerves.

XII. Thor.	XII. Rib.
I. Lamb.	'Subcostal.
II. Lamb.	>hypogastric. >lingual.
III. L.	iral. schen.
IV. L.	utaneous.
Nervus farcalis. V. L.	Ant. crural.
Lumbo-sacral cord. I. Sacral.	sensory obturator. turator.
II. Sacral.	
III. S.	atic.
Bladder (inflated).	pubic. tum (inflated).

FIG. 1.—Dissection of lumbo-sacral plexus from in front.

Several fresh full-time fetuses were dissected immediately on receipt, at as rapid a rate as possible; the defined lumbar plexus and sympathetic cord, with their connections, having been first sketched, were removed 'en masse' and placed in a 1 p.c. solution of osmic acid for twenty-four hours; from this fixing and stain-

ing reagent, they were then transferred to 30 p.c. alcohol for several hours, which had the effect of darkening the osmic staining. The stained plexus, with its connections, was then pinned-out according to the sketch of its original position, and its various rami lettered on both the actual plexus and the sketch by corresponding signs. A part of each of the rami was then removed, its areolar sheath stripped off by needles, and its fibres teased out; the aim being to spread out in regular rows, to facilitate microscopic examination, and counting.

This method of investigation was used, in all, in six cases; which, from the cases in which both sides could be worked, produced ten plexuses. The subjects used were in four cases full-time stillborn foetuses; whilst the remaining two subjects were from infants aged ten months and two years.

Appended are the drawings of the various dissections. To each of these is affixed an analytical table giving the results of the examination of each ramus; and from these analyses a general table has been prepared which states the form of plexus examined, the number of white nerves found connected with each spinal nerve, and the average number for each spinal nerve, from nerves 19 to 24 inclusive.

From the following table it will be seen that there is a marked and sudden change in the character of the constituents of the rami in connection with the 22nd and 23rd spinal nerves, which nerves are in most cases the 2nd lumbar and 3rd lumbar respectively.

The ramus of the 22nd contains very many medullated fibres which have a characteristic small size (1.3μ to 3μ), and which are arranged in characteristic bundles: these number on the average over 200 fibres; whilst the rami of the 23rd nerves contain but few medullated fibres, and these are of a quite different character, being either of a considerably larger size, or else of a medium or very small size, and *scattered* at intervals throughout the mass of the non-medullated fibres, in a manner which distinguishes them from the typical bundles of small white efferent fibres of a white ramus.

The existence of similar white fibres in the grey rami below lumbar II. of the dog has been referred to above, and the explanation of their presence by Langley and Edgeworth given

TABLE OF MEDULLATED FIBRES IN RAMI.

Mark of Subject.	Sex.	Length or Age.	Side of Body.	Form of Plexus.	Nerve 19 = XI. Thor.		Nv. 20 = XII. Thor.		Nv. 21 = I. Lumb.		Nv. 22 = II. Lumb.		Nv. 23 = III. Lumb.		Nv. 24 = IV. Lumb.	
					No. of Rami.	No. of White Fibres.	Rami.	Fibres.	Rami.	White Fibres.	Rami.	White Fibres.	Rami.	White Fibres.	Rami.	White Fibres.
A	♂	52 cm.,	R.	Medium-low. No com. fr. XII. to 1st L. Nv. furcals < 1/4 4th L.	1	75	2	325	2	270	2	30	1	20
			L.	Do. do.	1	200	5	485	2	145	1	20	1	45
X	♀	Æt. 10/12,	R. only	? prob. 'high' from size of Nv. furc.	1	150	2	375	1	10	1	40
B	♂	50 cm.,	R.	Low. No com. fr. XII. to 1st Lumb. Nv. furcals < 1/4 IV. Lumb.	2	375	1	150	2	170	1	20	2	35
			L.	Do. do.	2	250	3	470	3	190	1	8	1	12
C	♀	53 cm.,	R.	Very high from absence of XII. Rib. Plexus begins with 20th Nerve.	1	135	(Nv. 20 = I. L.) 2	310	(Nv. 21 = II. L.) 3	510	(Nv. 22 = III. L.) 3	190	(Nv. 23 = IV. L.) 1	31	(Nv. 24 = V. L.) 1	12
			L.	Do. do.	2	230	3	245	1	350	2	94	2	20	1	4
D	♀	Æt. 2 years,	L. only	Medium. Com. fr. XII. to I. Lumb. Nv. furcals > 1/4 IV. L.	2	150	3	350	1	260	1	45	2	50
			R.	High. Ilio-hyp. fr. XII. Thr. No com. XII. to I. Lm. Nv. furc. < 1/4 IV. Lm.	2	175	1	300	1	300	1	15	1	2
E	♀	50 cm.,	L.	Medium. Com. fr. XII. Thr. to I. Lm.	2	225	2	550	3	175	1	8	1	10
			Averages:—		180	223				334		209		19		23

From this we may conclude:—

That the caudal limit of the lumbar efferent visceral nerves in man is at the level of the 22nd spinal nerve, which nerve is usually the 2nd lumbar.

The anomalous features seen in foetus C are of interest. Here the absence of the XII. rib on each side causes the

Nv. fore.	.	
V. L.	. . .	
Lumbo-sac.		
cord.		
I. Sacral.	.	
II. Sac.	--	
III. S.	--	St. sciatic.
IV. S.	---	
V. S.	---	Pubic.
I. Coccygeal.		Nv. erigens.

FIG. 2.—View of sacro-coccygeal plexuses (ant.).



FIG. 3.—Connections of nv. erigens of right side, teased out. $\times 5$.

diaphragm to receive an attachment to the column one vertebra higher than usual; this causes the anatomical thoracic nerves to cease at the 19th spinal nerve or XI. thoracic, which now becomes the subcostal nerve, whilst what should be the XII. thoracic nerve becomes incorporated into the lumbar plexus

forming the I. lumbar nerve, and giving rise to the ilio-hypogastric, ilio-inguinal, and partly to the genito-crural nerves. The whole extent of column and cord is, however, not shortened, for there are six vertebræ having lumbar features, and the extra pair of 'lumbar' nerves thus produced, as in a normal plan, are utilised in the plexuses. The 24th and 25th—here V. and VI. lumbar nerves—have normal characters in their forming the lumbo-sacral cords. The extra nerve offset to the plexuses is absorbed by the spreading out of the plexuses, and the production of extra nerves to the upper crural regions.

A question at once arose as to what effect this anomaly would have upon the splanchnic efferent offset. Examination showed that no material variation was produced. The small white fibres continued to pass from the cord as far as the 22nd spinal nerves as usual, the rami of the 22nd nerves were typical white rami: the only alteration that could be noted from an ordinary ramus of that root was, that the number of white fibres was slightly below the average.

This irregularity shows the importance of numbering nerve roots from the first spinal nerve downwards, rather than from more or less arbitrary descriptive marks.

A beginning was made to pursue a like investigation into the offset of the pelvic splanchnics: only two specimens, however, were worked out, and one of these with but poor results. The single case of use showed an origin from the 3rd and 4th sacral nerves, and none from the 2nd or 5th sacral (figs. 2 and 3).

3. *Anatomical Notes.*

A few remarks may be made here on the general anatomical arrangements of the lumbar rami and ganglia. Quain (11) says, "the ganglia are small . . . commonly four are, but a less number may be, present. . . . There are generally two connecting branches to each ganglion, but the number is not so uniform as in the chest." I found that a typical or symmetrical arrangement was the exception. On the right side of C (fig. 9) as many as eight ganglia were present, and the numerical arrangement of the rami was even more variant; four rami to a ganglion was common; in one case five were present (A, left, fig. 6); also the

I. lumbar nerve of the same specimen had five rami in connection therewith.

In one case the gangliated cord was doubled for a short distance, and two ganglia were found parallel to each other (C, right, fig. 9). The plexuses shown in fig. 1 approached nearest the average arrangement.

The relations of the rami were usually as described by Quain: "they cross the bodies of the vertebræ, are covered by the fibrous bands which give origin to the muscular fibres of the psoas," but in about four cases the rami were found to traverse the fleshy origin of the psoas, instead of being beneath the fibrous arches.

Further, it will be noted from the comparison of figures and analyses how mixed are the white and grey fibres within the efferent limits; that is to say, one cannot speak of a white ramus or of a grey ramus as existing in this region, but merely of the predominance of white or grey fibres, as the case may be.

In concluding, I wish to state that I am indebted to Professor Kanthack for his kindness in procuring me necessary material for dissection; and to Mr H. K. Anderson for many hints on technique, which his long experience in such matters rendered particularly useful.

The following are the tracings of the plexuses described:—

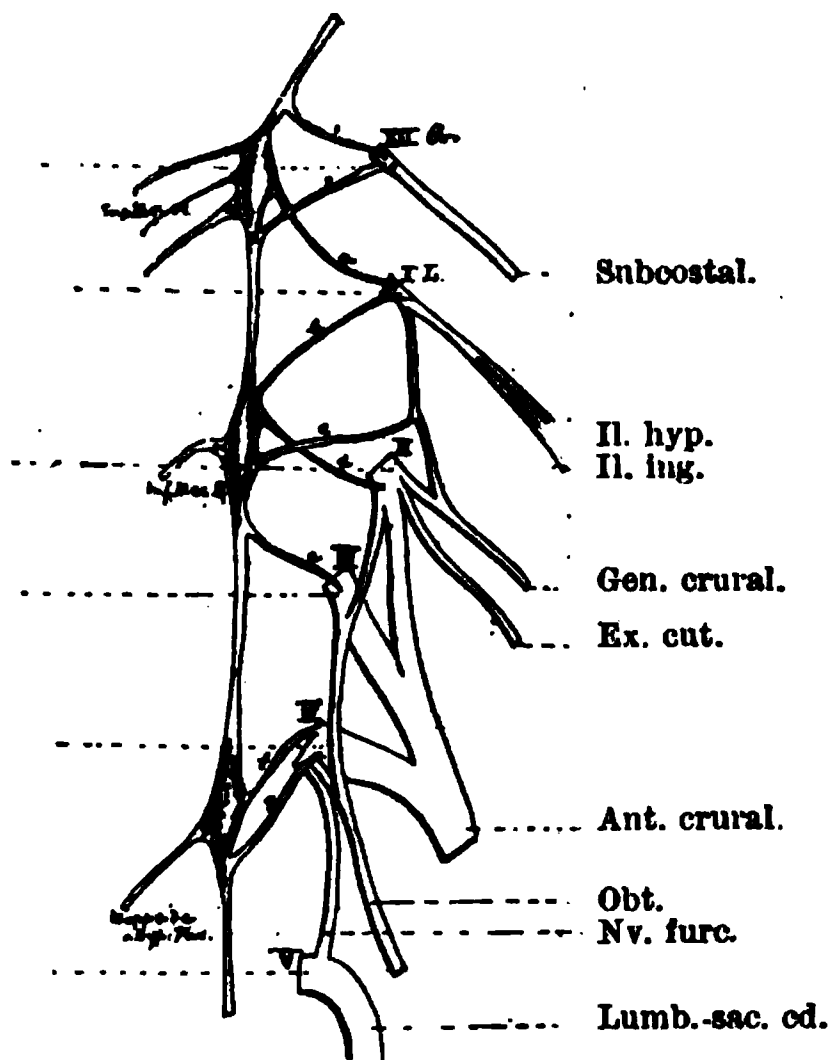


FIG. 4.—‘D,’ ♀, æt. 2 years (fragment from mortuary), left side.

Analysis.

Nerve Root.	Ramus.	Number of White Fibres.	Description.
XII. Th.	1	100	Half white, half grey.
XII. „	2	50	$\frac{3}{4}$ grey.
I. Lm.	a	6	Almost all grey.
I. „	b	350	White, with many grey.
I. „	c	140	Only few grey.
II. „	d	120	„
III. „	e	45	Very large grey ramus.
IV. „	f	50	„
IV. „	g	20	Small „ grey ramus.

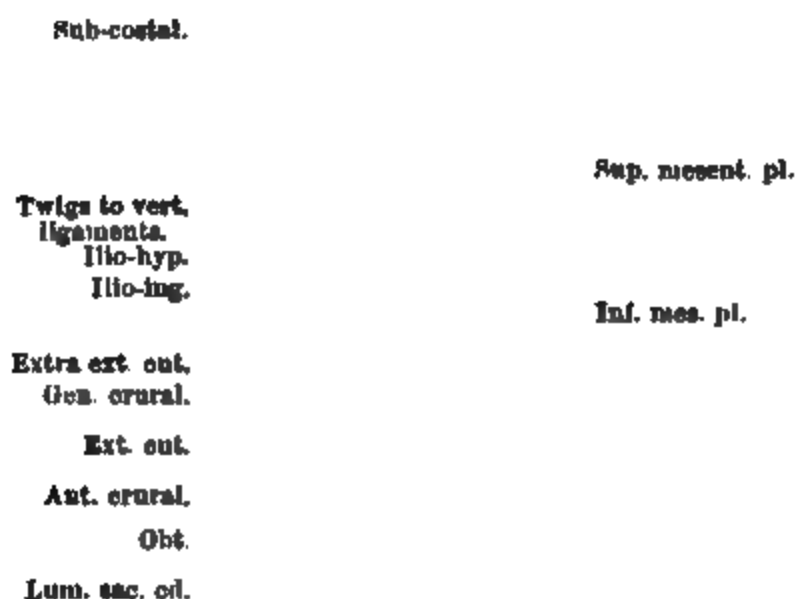


FIG. 5.—'A,' ♂, 52 cm. long, right side.

Analysis.

Nerve Root.	Ramus.	Number of White Fibres.	Description.
XII. Th.	a	75	Mostly white, $\frac{1}{10}$ grey.
I. Lm.	b	25	Mostly grey.
I. "	c	300	Mostly white, few grey.
II. "	d	20	About $\frac{1}{2}$ white, $\frac{1}{2}$ grey.
II. "	e	250	Very few grey.
III. "	g	30	Large grey ramus, few scattered white.
IV. "	h	20	Medium grey ramus, white fibres scattered.

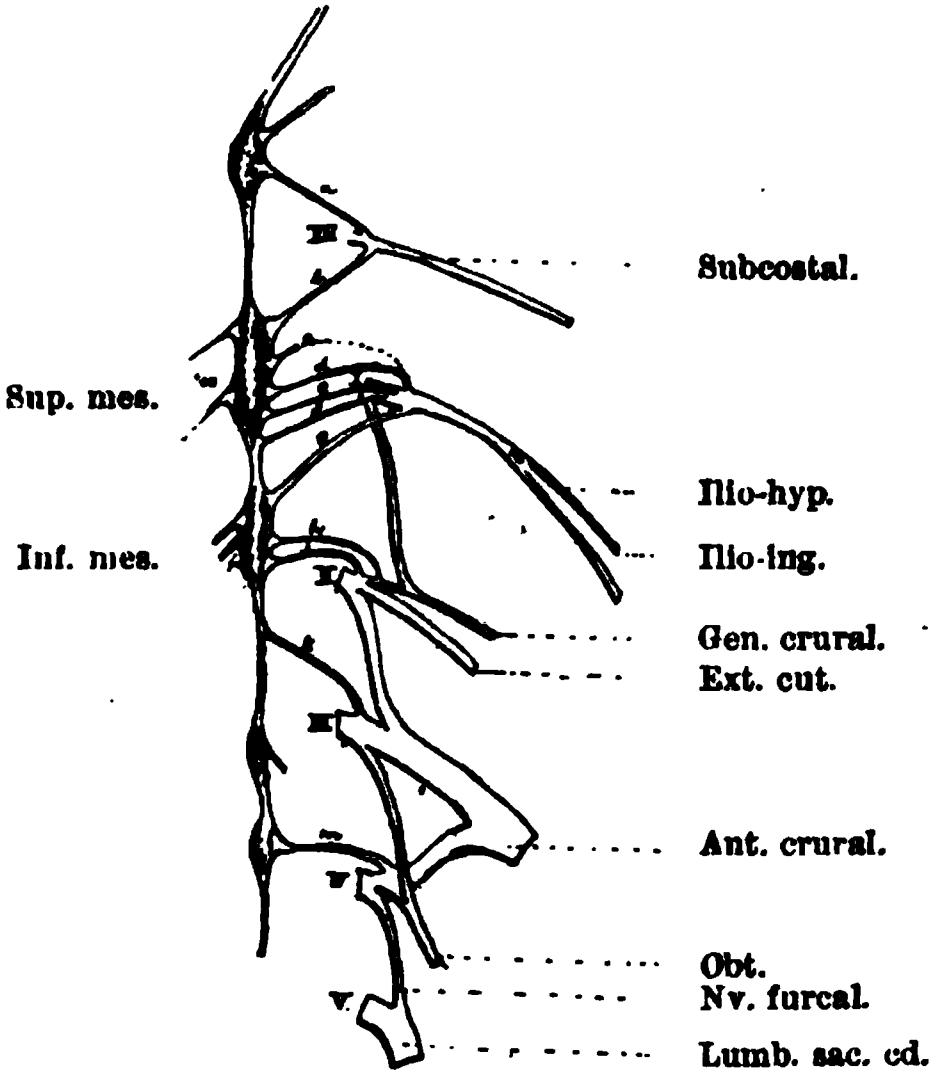


FIG. 6.—'A,' ♂, 52 cm. long, left side.

Analysis.

Nerve Root.	Ramus.	Number of White Fibres.	Description.
XII. Th.	<i>a</i>	150	Very few grey.
XII. „	<i>b</i>	200	„
I. Lm.	<i>c</i>	150	„
I. „	<i>d</i>	50	Half white, half grey.
I. „	<i>e</i>	100	Almost all white.
I. „	<i>f</i>	10	Large grey ramus.
I. „	<i>g</i>	175	Only few grey.
II. „	<i>h</i>	120	„
II. „	<i>j</i>	25	Mostly grey.
III. „	<i>k</i>	20	Grey ramus.
IV. „	<i>m</i>	45	„

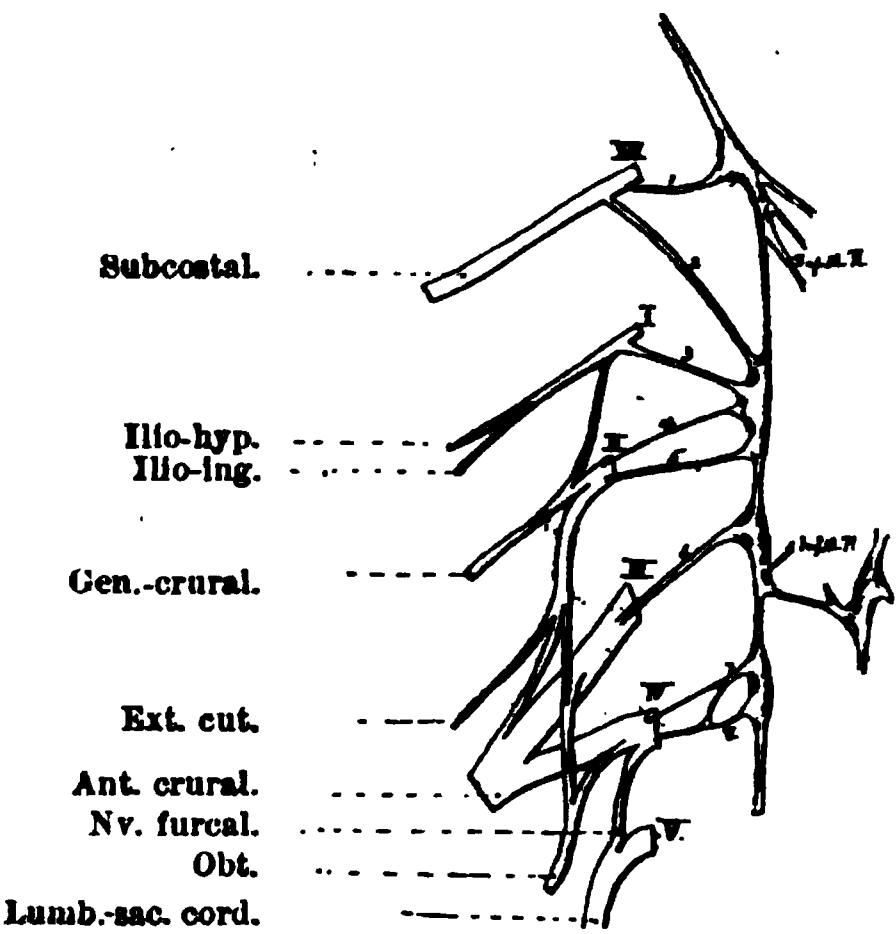


FIG. 7.—' B,' ♂, 52 cm. long, right side.

Analysis.

Nerve Root.	Ramus.	Number of White Fibres.	Description.
XII. Th.	1	175	Mixed.
XII. "	2	200	Grey, few.
I. Lm.	3	150	"
II. "	4	50	$\frac{2}{3}$ Grey.
II. "	5	120	Almost all white.
III. "	6	20	Grey ramus.
IV. "	7	15	"
IV. "	8	20	"

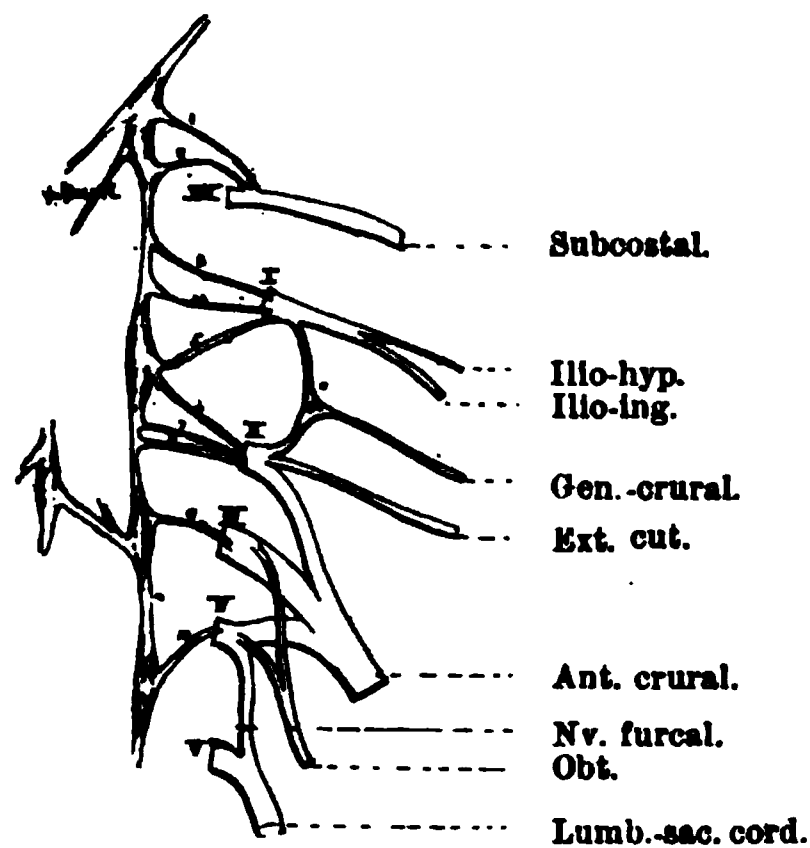


FIG. 8.—‘B,’ ♂, 52 cm. long, left side.

Analysis.

Nerve Root.	Ramus.	Number of White Fibres.	Description.
XII. Th.	1	50	About $\frac{2}{3}$ grey.
XII. „	2	200	About $\frac{1}{3}$ grey.
I. Lm.	3	120	Half white, half grey.
I. „	4	150	Very few grey.
I. „	5	180	Double ramus, each with few grey.
II. „	6	90	$\frac{1}{8}$ grey.
II. „	7	50	About $\frac{3}{4}$ grey.
II. „	8	50	Half white, half grey.
III. „	9	8	Grey ramus.
IV. „	10	12	„

(XI, 4th costal.

II. hyp. + II. long.

Extra genital.

Extra ext. cut.

(Gen. crural.

Ext. cut.

Ext. crural joins
ant. div.; ant.
crural in thigh.

Ant. crural

(Nt.

Nv. furcal.

Lumb. sac cord.

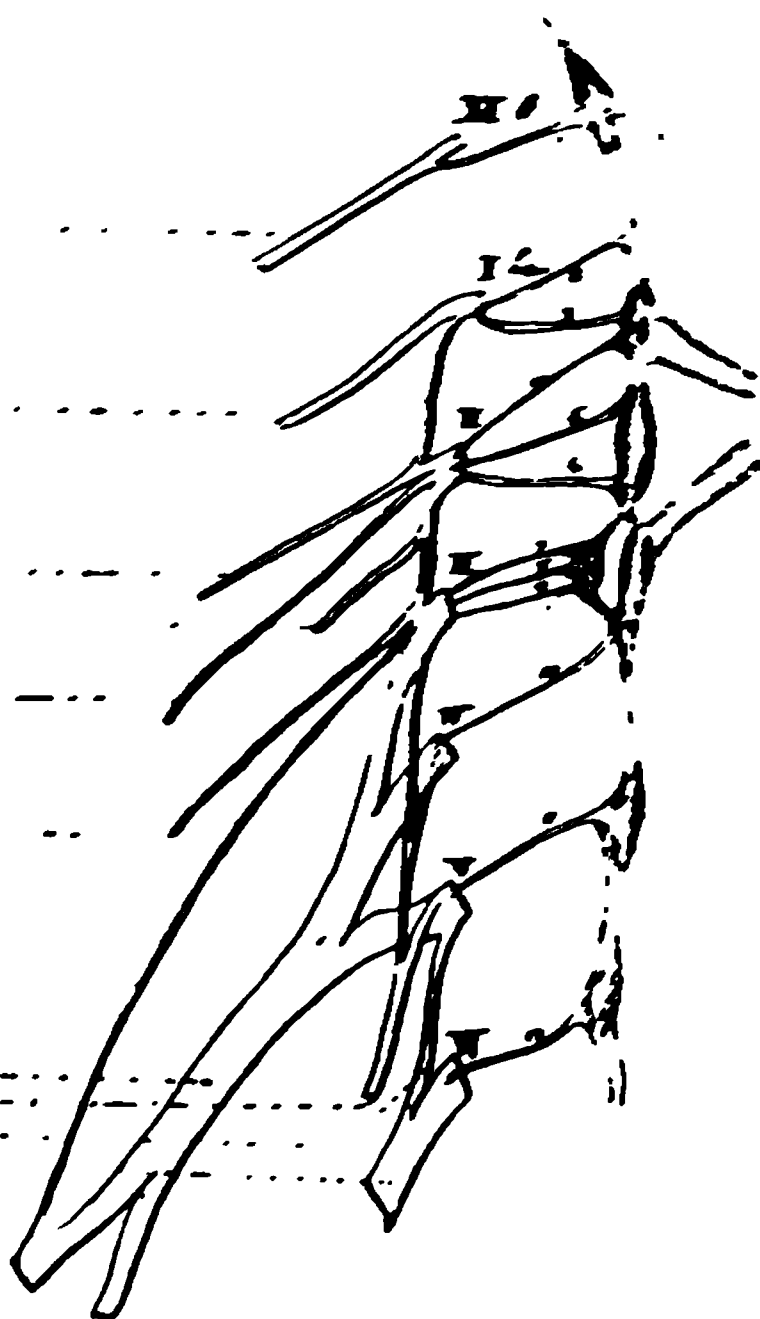


FIG. 9.—'C,' ♀, 53 cm. long, right side. (XII. rib absent, and consequent anomalous plexus.)

Analysis.

Nerve Root.	Ramus.	Number of White Fibres.	Description.
XI. Th.	1	135	Few grey.
I. Lm.	2	120	"
I. "	3	190	"
II. "	4	240	Half white, half grey.
II. "	5	20	Mostly grey.
II. "	6	290	Almost all white.
III. "	7	50	$\frac{1}{3}$ grey.
III. "	8	30	Small ramus, half grey.
III. "	9	40	Half grey.
IV. "	10	31	Grey ramus, white fibres scattered.
V. "	11	12	" "
VI. "	12

- Subcostal.
- II. hyp. and II. ing.
- Gen. crural.
- Extra crural cutan.
- .. Ext. cut.
Extra crural joins ant. div.;
ant. crural in thigh.
- .. Ant. crural.
- .. Obt.
- .. Nv. farcal.
- ... Lumbo.-sac. cord.

FIG. 10.—'C,' ♀, 53 cm. long, left side. (XII. rib absent, and consequent anomalous plexus.)

Analysis.

Nerve Root.	Ramus.	Number of White Fibres.	Description.
XI. Th.	1	30	Mainly grey.
XI. "	2	200	Half white, half grey.
I. Lm.	3	150	About $\frac{2}{3}$ grey.
I. "	3a	50	"
I. "	4	45	Small ramus, very few grey.
II. "	5	{ 230 120 }	Double. Few grey in each.
III. "	6	34	Small ramus, half white, half grey.
III. "	7	60	Small ramus, about $\frac{1}{3}$ grey.
IV. "	8	15	Grey ramus.
IV. "	9	5	"
V. "	10	4	"
VI. "

Subcostal.

II. hyp., derived
from subcostal.
II. ing.
G.-Cr. { Genital nv.
 { Crural nv.
 Ext. cut.
 Obt.
 Nv. furcal.
Lumb.-sac. cord.

Ant. crural.
Mid. cut. of ant.
crural.

obturator.

acilla.

Passed between pectinens and il. paves
muscles to hip-joint.

FIG. 11.—'E,' ♀, 50 cm. long, right side.

Analysis.

Nerve Root.	Ramus.	Number of White Fibres.	Description.
XII. Th.	1	100	Mostly white.
XII. "	2	75	Half white, half grey.
I. Lm.	a	200	About $\frac{1}{3}$ grey.
II. "	b	300	Very few grey.
III. "	c	III	Large grey ramus.
IV. "	d	2	" "
V. "	e	18	Medium grey ramus.

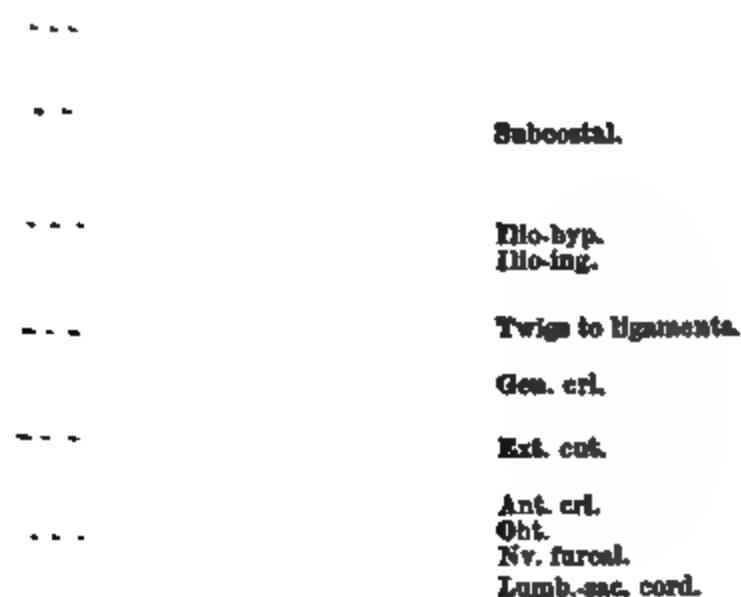


FIG. 12.—'E,' ♀, 50 c.m. long, left side.

Analysis.

Nerve Root.	Ramus.	Number of White Fibres.	Description.
XII. Th.	1	150	Mostly white.
XII. "	2	75	Half white, half grey.
I. Lm.	a	250	Very few grey.
I. "	b	100	About $\frac{1}{3}$ grey.
II. "	c	45	About $\frac{2}{3}$ grey.
II. "	d	120	Very few grey.
II. "	e	10	Large ramus, almost all grey.
III. "	f	8	Small grey ramus.
IV. "	h	12	Grey ramus.

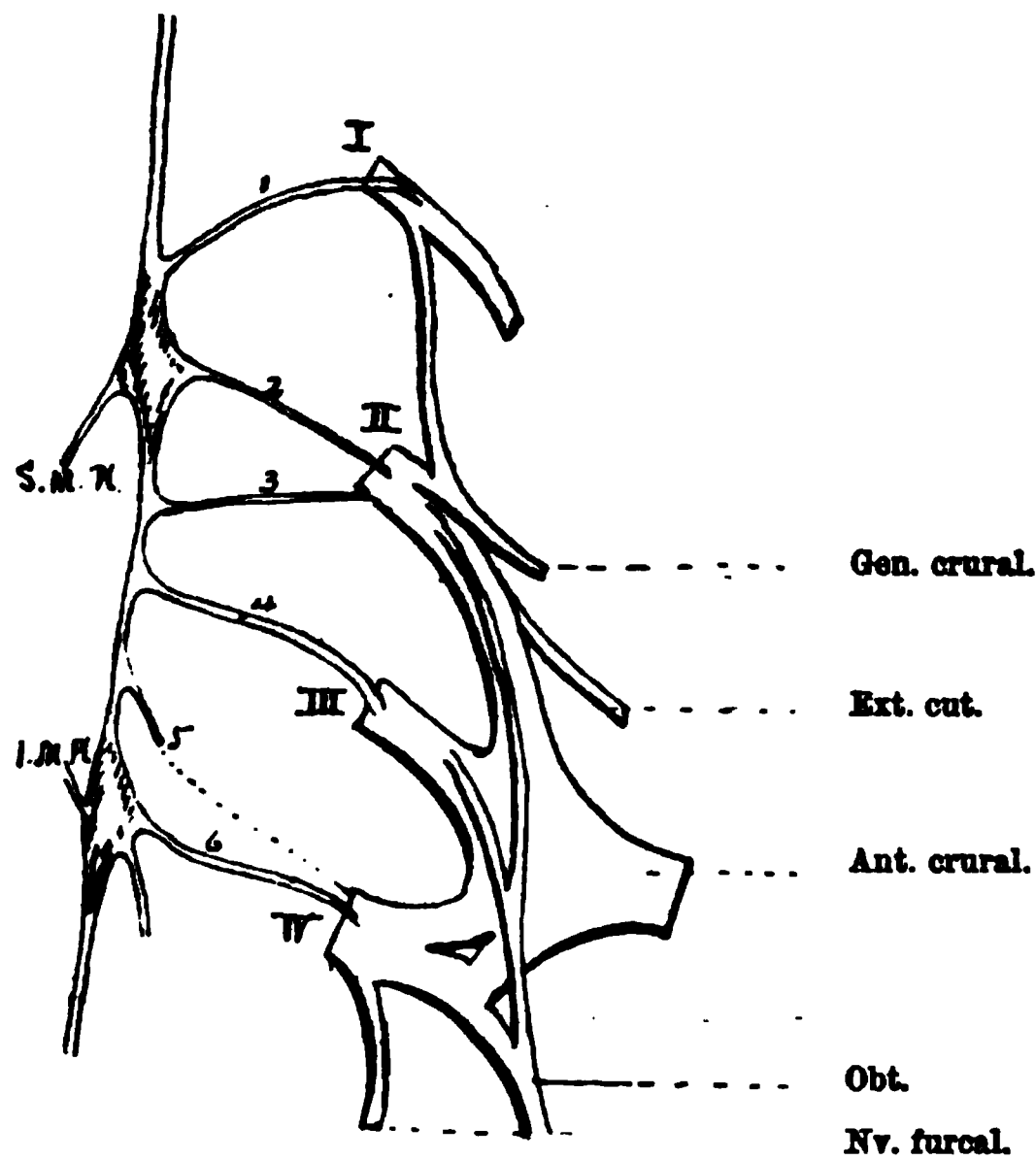


FIG. 13.—'X,' ♀, set. 9/12, left side (fragment from case reported *Journal of Anat.*, January 1898).

Analysis.

Nerve Root.	Ramus.	Number of White Fibres.	Description.
I. Lm.	1	150	Mostly white.
II. „	2	75	Half white, half grey.
II. „	3	300	Very few grey.
III. „	4	10	Grey. White fibres, large and scattered.
IV. „	5	30	Grey.
IV. „	6	10	„

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ON THE ANATOMICAL STRUCTURE OF THE VAGUS NERVE. By WAKELIN BARRATT, M.D., *Technical Research Scholar to the London County Council.* (PLATES VIII.–XII.)

(From the Pathological Laboratory of the London County Asylums.)

WHILE recently engaged in investigating the condition of the vagus nerve in general paralysis of the insane and in beriberi, I undertook, at the suggestion of Dr Mott, in order to facilitate this examination, a further investigation into the normal anatomy of this nerve, and in this way many facts were ascertained which have not, so far as I can discover, been hitherto described. These details of structure are of interest to the physiologist, and a knowledge of them is indispensable when a complete examination of the vagus in pathological states is attempted.

Ten vagus nerves were examined in their course from the jugular foramen above to the root of the lung below. Transverse sections of the nerves were made in different situations, namely, where the superior laryngeal branch leaves the main trunk, and at various points above this level; at the point of divergence of the inferior laryngeal, and below this level; as well as at a point between these two levels. Sketches of the appearances presented by the transverse sections (figs. 1, 2, 3, and 4) were made accurately to scale, and were arranged side by side in a descending series, for the sake of ready comparison. Transverse sections of the laryngeal and other branches were also made separately at the above-mentioned levels, in order to check the conclusions arrived at as to the position of these branches in the main trunk. In addition, longitudinal sections were made, corresponding to the transverse ones. The stains found most useful were osmic acid, methylene blue, and safranin. Immediately after death the cadavera were, in accordance with the usual mortuary routine, placed in a chamber maintained at 28° F. to 30° F. until the post-mortem examination took place.

By a study of transverse sections made as above described, the

following facts respecting the constitution of the vagus nerve were elicited. The vagus was found to be made up of bundles of nerve-fibres which present the peculiarity of being repeatedly rearranged as the nerve travels onward, so that the appearance of transverse sections (cp. figs. 1 and 2, C to F) is constantly altering, even at closely contiguous levels; that is, at levels which above the inferior ganglion are only a few millimetres apart, and in the neck are separated by a few centimetres. This rearrangement may be compared to that which occurs in the plexuses formed by the spinal nerves; for instance, the brachial plexus. And inasmuch as the appearance presented by sections at the same level (figs. 1 to 4) varies considerably in different nerves, particularly as to the size, number, and arrangement of the nerve-bundles, and the extent to which these coalesce with, or remain separate from, each other, it would appear that the arrangement of the nerve-bundles is not confined to a single type, but that several modes of arrangement are possible, as in the case of the brachial plexus already referred to.

At the level at which the superior laryngeal nerve (*sup. lar. n.*) leaves the main trunk (C, figs. 1 to 4), the inferior laryngeal nerve (*rec. lar. n.*) can also be recognised. The identification of the laryngeal nerves (and the same applies to other nerves whose position in the main trunk it may be desired to recognise) is made by a comparison of the mixed nerve with sections of the laryngeal nerves made separately, especial attention being paid to the size of the nerve-bundles, the thickness of their nerve-sheaths, and the character and arrangement of the septa within; and to the relative preponderance of medullated fibres in these nerves. If the inferior laryngeal breaks up early into smaller bundles, it may also be necessary to cut sections of the main trunk at levels intermediate between those of the divergence of the superior and inferior laryngeal nerves respectively, so as to follow the latter nerve upwards in the trunk of the vagus. The fact that the two laryngeal nerves can be recognised at the same high level is important, in view of the distribution of both to the same region.¹

The vagus nerve varies in sectional area in different cases.

¹ Both nerves, however, contain cardiac branches. In the superior laryngeal a small collection of non-medullated fibres runs in the crico-thyroid nerve (this

Sometimes, when two vagus nerves from different subjects are contrasted in transverse section, the one may show at every level a distinctly smaller sectional area as compared with the other. The explanation of this difference is, perhaps, to be found in the circumstance that the vagus is readily stretched during removal, or in hardening if small weights are attached to the nerve.

The nerve-fibres of the vagus have been classified by Gaskell¹ into large medullated, which are about 10.8μ in diameter, small medullated, and non-medullated. My own observations (cp. figs. 5, 6, and 7) give similar results, the size of the large medullated varying from 8.7μ to 12μ , that of the small medullated being 3.5μ to 7μ , or even 8μ , and the non-medullated ranging from 1μ or 2μ to 4μ . The large medullated fibres contain relatively more myelin than the small medullated fibres, which thus appear to be constructed on a different type. The small medullated fibres, also, like the non-medullated, are very apt to exhibit varicosities, while the neighbouring large medullated fibres, though their outlines may here and there be wavy or irregular, yet remain, on the whole, much more free from distortion than the smaller fibres.

A study of transverse sections shows that the relative proportion of medullated and non-medullated fibres varies in different parts of the vagus. In the pharyngeal and also the laryngeal branches (particularly the superior laryngeal, cp. fig. 5) large medullated fibres are conspicuous;² in the main trunk of the vagus (fig. 6) small medullated and non-medullated fibres are abundant; the thoracic cardiac (fig. 7) and pulmonary nerves not unfrequently consist of non-medullated nerves, either pure or mixed with a very few small medullated fibres. Collections of non-medullated nerve-fibres are not uncommon in the main trunk

nerve is seen on the left imperfectly separated from the main trunk of the superior laryngeal nerve in C, fig. 2), and goes to join the cardiac branch given off from the upper cervical ganglion of the sympathetic. The cardiac nerves in the inferior laryngeal are much more numerous: they separate from the inferior laryngeal soon after its divergence from the main trunk, as shown in the diagram of the vagus accompanying figs. 1 to 4.

¹ "On the Relation between the Structure, Functions, Distribution and Origin of the Cranial Nerves; together with a Theory of the Nervous System of Vertebrata," *Jour. of Physiol.*, vol. x., 1889, pp. 153-212.

² The same is true of the branches of distribution of the glosso-pharyngeal, spinal accessory, and the hypoglossal.

at all levels, and sometimes in its larger branches, particularly the inferior laryngeal. These fibres of Remak are usually situated on the periphery, but are occasionally surrounded by mixed fibres (E, fig. 4). They seem generally to be on the point of leaving the nerve, to proceed to their area of distribution.

The appearance of the inferior ganglion of the vagus varies in different nerves. Transverse sections of the vagus at the level of this ganglion (figs. 1 to 4 at level B) sometimes exhibit a large main trunk containing nerve-cells surrounded by a few smaller bundles of nerve-fibres, as in fig. 3, B; sometimes the main trunk is small, and the surrounding nerve-bundles are of correspondingly larger size, as in fig. 2, B. In the former case the ganglionic mass is seen to occupy only a portion of the main trunk; in the latter case the nerve-cells are more evenly diffused through the whole, but in each case only a portion of the nerve-fibres goes through the ganglion, the remainder passing by the side of the ganglion. Nevertheless, in transverse sections of the vagus, nerve-cells are seen occasionally in the outlying bundles of nerve-fibres; and as these are repeated in successive sections, it follows that they are arranged in slender columns. From the main mass of ganglion-cells also sometimes one or several small columns of cells descend for some distance in the main trunk of the nerve, below the level at which the superior laryngeal diverges. Our conception of the inferior ganglion of the vagus is therefore not a simple one. It sometimes consists of an elongated mass of cells in the upper part of the main trunk of the vagus, while at other times it includes in addition separate slender cell-columns in outlying nerve-bundles, at the same level (*e.g.*, the superior and inferior laryngeal nerves), and a downward continuation in the trunk of the vagus, in the form of one or more cell-columns, for some distance below the divergence of the superior laryngeal.

The inferior ganglion of the vagus is regarded by Gaskell¹ as a vagrant ganglion or anterior-root ganglion, and of the nature of a sympathetic ganglion. By Van Gehuchten² it is regarded as analogous to the ganglia on the posterior roots of the spinal nerves. In the circumstance, referred to above, that only a por-

¹ *Loc. cit.*, pp. 178-9.

² *Anatomie du système nerveux de l'homme*, Louvain, 1897, pp. 480, 481.

tion of the nerve-fibres, with which it is in relation, passes through the ganglion, it presents a striking resemblance to a posterior root ganglion, and a section through the vagus at the level of the inferior ganglion corresponds very closely to a section of a mixed spinal nerve taken through the ganglion on the posterior root.

The nerve-cells in the inferior ganglion of the vagus (fig 8) also closely resemble in appearance the cells of the ganglia on the posterior roots of the spinal nerves. They are surrounded by multi-nucleated capsules; and though it is generally difficult to recognise any nerve-processes, yet a few cells can be seen to exhibit a single thick process which curves over the cell, surrounded by a prolongation of the capsule. The cells vary considerably in size (from 18μ to 36μ), staining power, degree of pigmentation, and the presence or absence of a nucleus. They are frequently retracted from their capsules, when their outline may be sharp or rugged. In all these points the inferior ganglion of the vagus bears so close a resemblance to the ganglia on the posterior roots of the spinal nerves that it is difficult to believe that it is not homologous with the latter.

In one case the skull was opened from behind, the vagus dissected out, and transverse sections of it examined at intervals of $\frac{1}{2}$ mm. down to the level of the inferior ganglion. They showed that the two ganglia were separated by an interval of 3 mm. The upper ganglion was $1\frac{1}{2}$ mm. long, and the cells of the two ganglia were not obviously distinct in character.

This work has been done in the pathological laboratory at Claybury Asylum, and my warmest thanks are due to Dr Mott for his invaluable assistance throughout.

DESCRIPTION OF PLATES VIII.-XII.

Fig. 1. On the right is seen a diagram of the vagus nerve, from the base of the skull to the root of the lung, with its principal branches—namely, the pharyngeal nerve (*phar. br.*); the superior laryngeal nerve (*sup. lar. n.*); the inferior cervical cardiac nerve (*inf. cerv. card. n.*); the recurrent laryngeal nerve (*rec. lar. n.*); and the thoracic cardiac and pulmonary nerves (*card. and pulm. brs.*). Above, the glosso-pharyngeal nerve (*gl. ph. n.*), the spinal accessory nerve (*sp. acc. n.*), and the hypoglossal nerve (*hypogl. n.*) are indi-

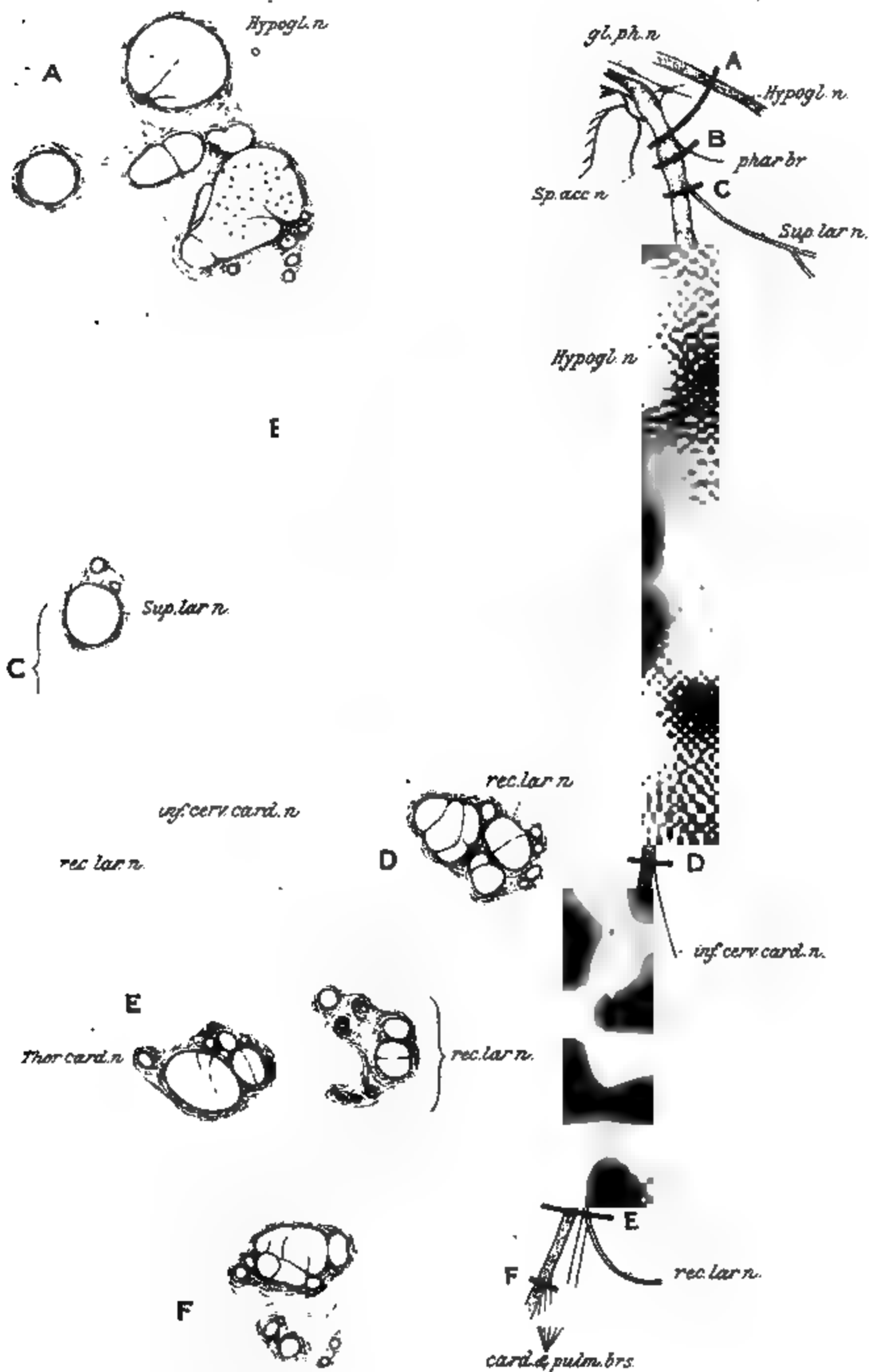


Fig. 1.

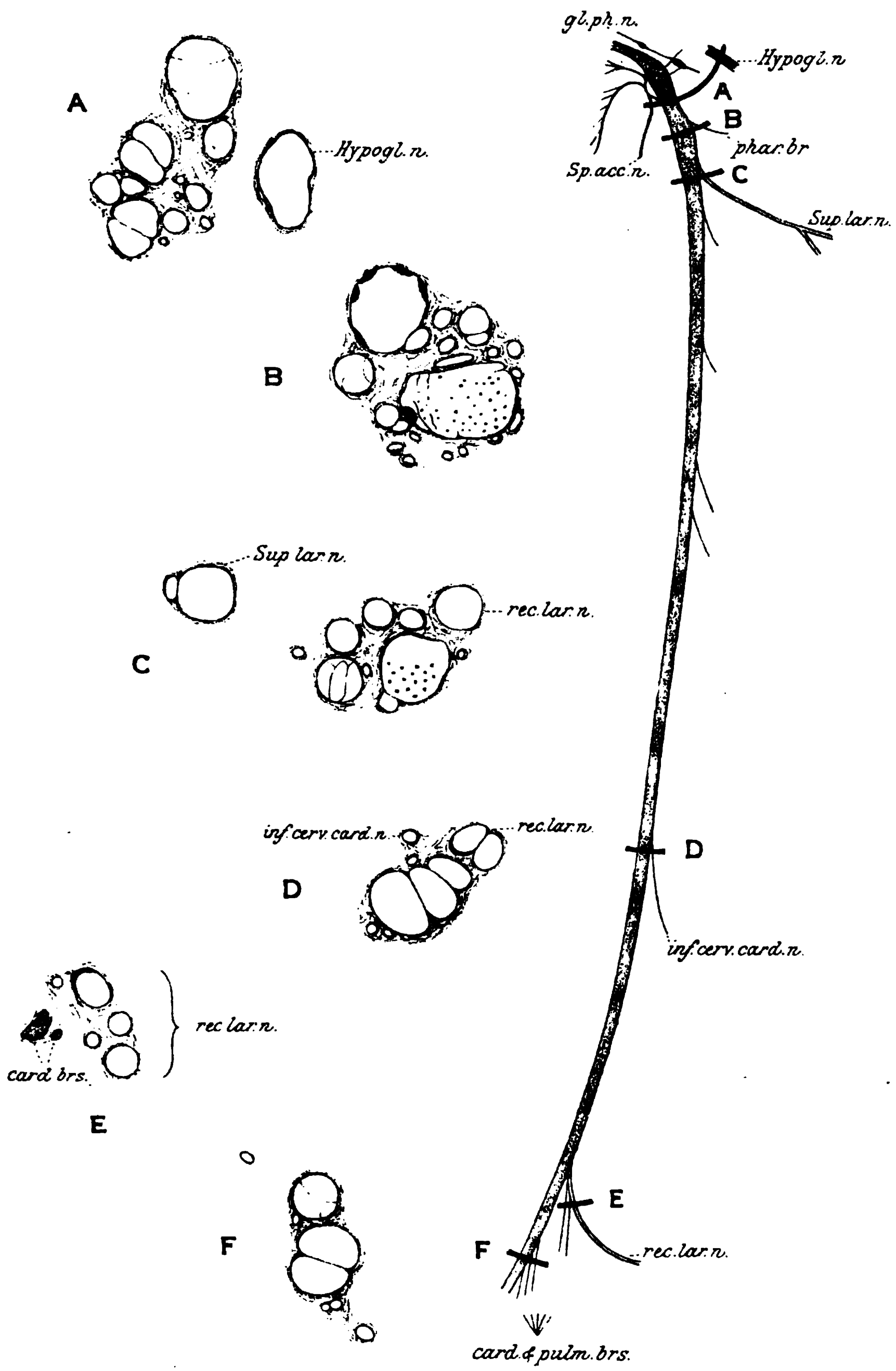


Fig. 2.

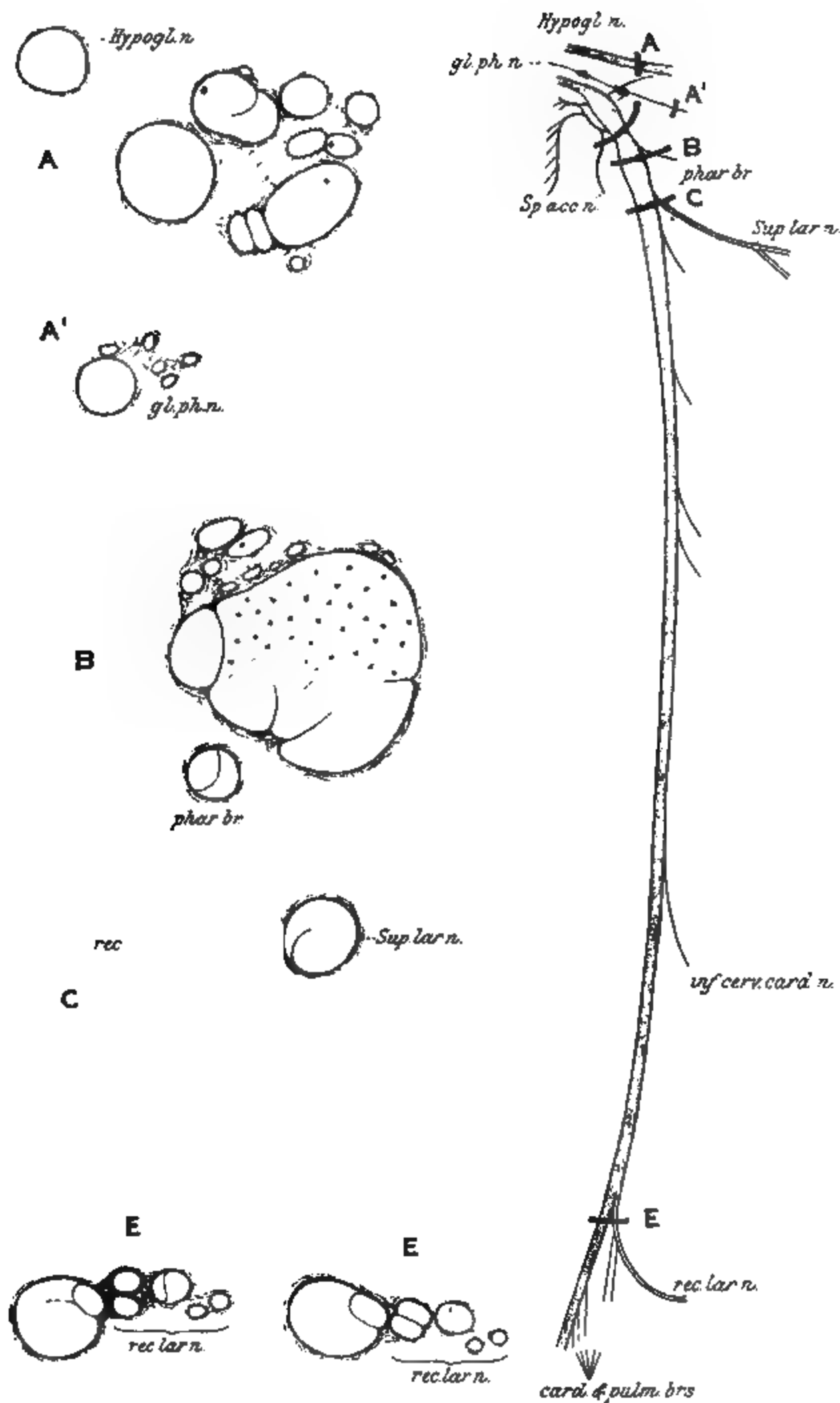


Fig 3.

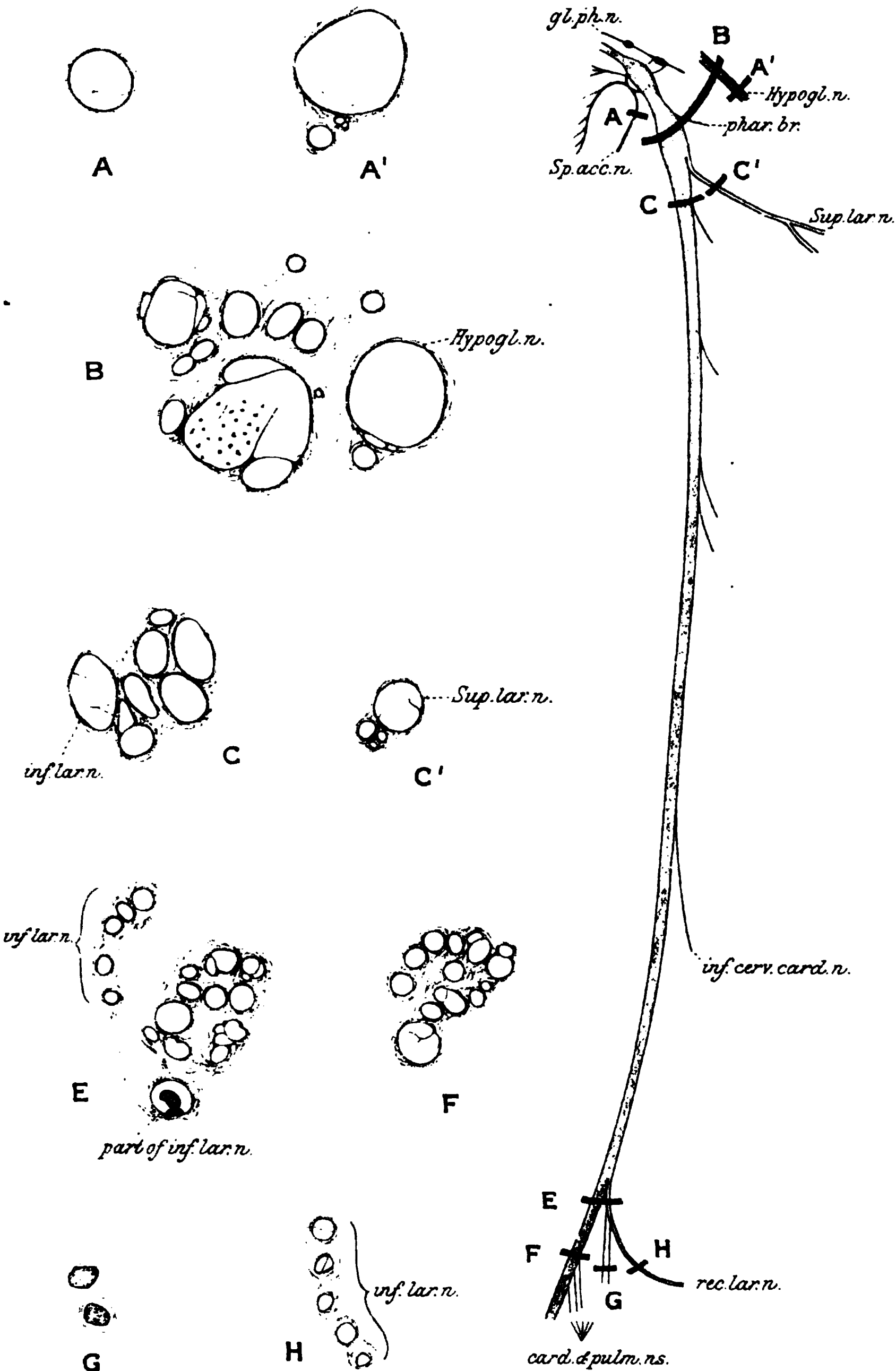


Fig. 4.



Fig. 5.

5

Fig. 6.

Fig. 7.

Fig. 8.

cated. The levels at which the transverse sections of the vagus are made are denoted by the thick black lines: A, above the inferior ganglion; B, through the middle of the inferior ganglion; C, at the point of divergence of the superior laryngeal nerve from the main trunk; D, at the point of divergence of the inferior cervical cardiac nerve; E at, and F below, the point of divergence of the inferior laryngeal nerve. This diagram is nearly of the natural size.

On the left are seen transverse sections of the vagus at the levels A, B, etc., all drawn to the same magnification, with such of the more important nerve-bundles as can be identified, indicated by the same lettering which is used in the diagram to the right. The nerve-cells of the inferior ganglion are shown in A and B. $\times 9$.

Fig. 2 is similar to the above. The shaded areas in B, D, and E indicate collections of non-medullated fibres, those in D and E going to the cardiac plexus. Nerve-cells in the main trunk are seen at C.

Fig. 3 is similar to the preceding. In the transverse sections at A, B, and C, single nerve-cells, representing cell-columns cut across, are seen in the outlying bundles of nerve-fibres; and at C, nerve-cells are again present in the main trunk, as in the preceding fig. There is less division of the main trunk into separated bundles than in the preceding figs., particularly at C and E.

Fig. 4 is similar to the preceding. At E, the trunk is divided into a large number of bundles. At E and G, collections of non-medullated fibres are indicated by the light shading,—one such collection at the lower part of E (below the main trunk) being placed centrally.

Fig. 5. Transverse section of part of the inferior laryngeal nerve. Large and small medullated nerves are seen—the former preponderating. Above and to the right some non-medullated nerves are seen, though somewhat indistinctly; elsewhere these fibres are not recognisable, having been obliterated during the preparation of the section. $\times 375$. Osmic acid. Safranin.

Fig. 6. Transverse section of the main trunk of the vagus at D (figs. 1 and 2). Large and small medullated, and non-medullated fibres are seen, the last predominating. The nuclei of the primitive sheaths of the non-medullated fibres are also seen. $\times 475$. Osmic acid. Safranin.

Fig. 7. Transverse section of a small thoracic cardiac nerve. The nerve is made up of non-medullated fibres, the nuclei of which are readily distinguishable; two small medullated fibres are shown near the centre. $\times 375$. Osmic acid. Safranin.

Fig. 8. Portion of a transverse section of the inferior ganglion of the vagus. Seven ganglion-cells are seen, varying considerably in their staining power, and exhibiting, with two exceptions, more or less faintly outlined nuclei. Three of the cells exhibit pigment-masses. The upper cells present an appearance of processes running between the body of the cell and the capsule. The capsules are multi-nucleated (the nuclei are not, however, so numerous as in the ganglia on the posterior spinal roots). Surrounding and separating the nerve-cells are numerous nerve-fibres, cut across transversely, most of which exhibit axis-cylinders. $\times 275$. Aniline-blue.

THE MUSCLES OF MAMMALS, WITH SPECIAL RELATION TO HUMAN MYOLOGY: A COURSE OF LECTURES DELIVERED AT THE ROYAL COLLEGE OF SURGEONS OF ENGLAND, by F. G. PARSONS, F.R.C.S., *Hunterian Professor*.

LECTURE I.—THE SKIN MUSCLES AND MUSCLES OF THE HEAD AND NECK.

MR PRESIDENT AND GENTLEMEN,—As the whole subject of mammalian myology is too large to be dealt with in three lectures, I have had some difficulty in making up my mind what points I should bring before your notice, and what I should leave out. It seemed to me that it would be more in keeping with the spirit of the man in whose memory these lectures are given if I laid special stress on the chief points which I have myself observed, and the deductions I have drawn from them.

If I fail to call sufficient attention to the writings of others, writings often more worthy of being recorded than my own, it is because I feel that the honour of a Hunterian Professorship of this College calls for as much original work as the holder is capable of giving.

The muscles to which I have decided to call your attention have been chosen, as far as possible, because they have some bearing on human myology; because they seem to explain either the constant arrangement of man's muscles, or the commoner variations met with in him. My own acquaintance with the muscles of monkeys and anthropoid apes has been greatly added to by the kindness of my friend Mr Keith, who has placed at my disposal a mass of, as yet, unpublished work on these animals.

I must disclaim any intention of giving a complete account of all that is known about any muscle: such a proceeding would not, I think, be suitable for a short course of lectures. I shall rather try to call your attention to certain disjointed facts which seem to me suggestive, and which I hope may prove interesting.

Panniculus carnosus.—This is found throughout the mam-

malia, and forms a more or less complete investment of the trunk, as well as being prolonged for some distance on the extremities. It is important to realise that this skin muscle consists of several layers, the fibres of which run in different directions. It thus happens that in some places as many as three, or even four, planes of fibres may be detected, while elsewhere it may be wanting entirely, and nothing intervenes between the skeletal muscles and the skin. In many places the panniculus becomes attached to subjacent bony points; and when these special fibres are of use to the animal, they increase and form bundles sufficiently marked off from the rest to induce an observer to give them a special name. Some of these bundles are of interest to the human anatomist, although I know of no mammal that is less well adapted for studying the skin muscles than man.

If we select a mammal in which the panniculus is fairly, but not very strongly, developed, such as one of the carnivores, a racoon for instance, we find the platysma running from the mouth region backward and upward, that is, dorsally and caudalward. Deep to this is another muscle which rises from the fascia over the masseter, and passes ventrally and caudalward, ending in the mid line of the throat, where it blends with its fellow of the opposite side: this muscle, from its appearance, is known as the sphincter colli. On the lateral part of the trunk of the same animal we find a layer of muscle which shades off into the skin posteriorly, while anteriorly it passes deep to the pectoralis major, to be inserted into the humerus. The dorsal part of this layer is known as the dorso-humeralis; the ventral part, feebly developed in carnivores, as the abdomino-humeralis. The dorso-humeralis, of course, lies superficial to the latissimus dorsi; and its fibres, to reach the humerus, have to wind round the ventral border of that muscle, and then cross the axilla. The shoulder region, it will be seen, has no panniculus at all over it (fig. 1).

A dissection of an ungulate would show nearly the same arrangement of dorso-humeralis, but the sphincter colli is ill developed, and in the horse there is a vertical bundle of fibres over the shoulder, which enables the animal to wrinkle the skin of that region in the manner familiar to everyone. If we next examine the panniculus of a rodent, a porcupine or guinea-pig for instance, we shall find that the platysma and dorso-humeralis are nearly identical with the same muscles in the carnivore, except that part of the latter is continued over the shoulder region, while the abdomino-humeralis is much more strongly developed and covers the external oblique muscle; as we trace it forward toward the pectoral, we find that, with care, it can be separated into two sheets, the more superficial of which passes ventral to the pectorals, while the deeper is interwoven with the fibres of

that muscle; we further see that there is no sharp line of demarcation between the abdomino- and dorso-humeralis. The sphincter colli in rodents rises from the fascia over the masseter, as in carnivores,



FIG. 1.—Panniculus of Raccoon (*Procyon*). a, platysma; b, sphincter colli; c, dorso-humeralis; d, abdomino-humeralis.

but, as a rule, the muscle, instead of being inserted into the mid line of the throat, is continued to the anterior part of the manubrium sterni, and consequently Dobson proposed the name of 'sterno-facialis' for it; this arrangement is very well seen in *Octodon*, one of the

THE PANNICULUS
OF THE RACCOON

FIG. 1

A

FIG. 2.—Platysma (A) and Sterno-facialis (B) of *Octodon*. (From the *Proceedings of the Zoological Society*.)

porcupine-like rodents (fig. 2). The strand mole or mole rat (*Bathyergus maritimus*) shows us that the sterno-facialis of rodents and the sphincter colli of carnivores are one and the same muscle. Here some of the fibres are inserted in the mid line of the throat, while the more

FIG. 3.—Panniculus of Strand Mole (*Bathyergus*).

a, platysma; *b*, sterno-facialis muscle; *b'*, sterno-facialis cut; *b''*, sterno-facialis cut; *b'''*, fibres decussating in mid line, foreshadowing the sphincter colli of the Primates; *c*, pectoral muscle; *c'*, branch of anterior thoracic nerve supplying the sterno-facialis; *d*, sterno-mastoid muscle; *e*, superficial fibres of the abdominal panniculus carnosus continuous with the sterno-facialis.

ventral part of the throat only, but the whole of the pectoral mass, and meets its fellow in the mid line from close to the symphysis menti to as far back as the xiphisternum (fig. 4). There can, I think,

be no doubt that this is the same muscle as the sphincter colli of the carnivore or the sterno-facialis of *Octodon* or *Bathyergus*. The dorso-humeralis is enormously developed, and most of its fibres pass over

FIG. 4.—Panniculus of Hedgehog (*Erinaceus*). *a*, sterno-facialis or sphincter colli; *b*, pectoral; *c*, abdomino-humeralis; *d*, dorso-humeralis; *e*, rectus ventralis.

the shoulder to the neck, where they fuse with the lateral part of the sterno-facialis, forming the huge sphincter muscle of the body which rolls the animal up into a ball, and which has so often been described.

The abdomino-humeralis is present, but is, in comparison, feeble: it passes entirely deep to the pectorals,—at least, I have never been able to find a superficial layer corresponding to that of *Bathyergus*. The ventro-humeralis and pectorals of all these animals are supplied by a large nerve which runs back (caudalward) from the internal cord of the brachial plexus. In the bats the platysma is extremely well marked, and is divided into two or three separate portions, but the sterno-facialis is entirely wanting as far as I have been able to find out (fig. 5). In the lemurs and cynomorphous monkeys the platysma is well developed, and reaches dorsally nearly to the mid dorsal line of the

FIG. 5.—Neck of Fruit Bat (*Pteropus*), showing tripartite platysma and absence of sphincter colli. *a*, *b*, *c*, platysma; *d*, parotid gland; *e*, *f*, slips of panniculus to patagium.

neck: it passes close behind the ear, and some of its anterior fibres in the lemur are evidently separated to form a transversus nuchæ. The sphincter colli, as Ruge has shown, is practically identical with that of carnivores. As the anthropoid apes are reached the sphincter colli disappears, until in man only vestiges of it remain. The abdomino-humeralis disappears in the primates, and probably becomes the sheath of the abdominal muscles; while the dorso-humeralis is present in lemurs and cynomorphous monkeys as a small flat muscle, lying superficial to the trapezius, and ending in a tendon which winds round that of the latissimus dorsi to cross the axilla, and become inserted into the humerus, in its usual place, deep to the pectorals (fig. 6). In the higher apes and man this too disappears.

Now to apply these facts to man. There can be little opposition to the view that the achselbogen or muscular slips so often found running across the axilla, and uniting the latissimus dorsi with the pectorals, are remains of the dorso-humeralis passing across from the superficial surface of the latissimus dorsi to the deep surface of the pectoral (fig. 6).

FIG. 6.—Axilla of Macaque Monkey. *a*, deltoid; *b*, pectoral; *c*, dorso-humeralis; *d*, latissimus dorsi; *e*, dorso-olecranal; *f*, biceps.

Ruge has shown that the transverse muscular fibres, which are sometimes found under the chin in man, superficial to the mylohyoid and digastric, are probably relics of the most anterior part of the sterno-facialis or sphincter colli; while I have contended that the musculus sternalis, that curious abnormality in man about which so much has been written, is nothing more than a survival of the thoracic fibres of the same muscle; and I think

that anyone who looks at the position and relations of the sterno-facialis of either the hedgehog or the African mole rat (*Bathyergus*) must be struck by the fact that if the neck portion (sphincter colli) were removed, a typical sternalis would remain (see figs. 3 and 4). The human sternalis is probably completed caudally by the superficial layer of the abdomino-humeralis, and this explains its tendency to merge in the fascia covering the abdominal muscles. In addition to this, a branch of the internal anterior thoracic nerve has been found piercing the pectoral in *Bathyergus*, and supplying the superjacent portion of panniculus. I am glad of the opportunity of advancing this theory again, because, since I first suggested it at a meeting of the Anatomical Society in 1895, I have been more and more convinced of its probability. The chief points made by those who do not agree with my views are, firstly, that a good explanation for the sternalis has already been given by Prof. Cunningham, who regards it as some of the fibres of the pectoral which have become twisted at right angles to their proper course; secondly, that in the animals nearest man—apes and monkeys—a sternalis has never been found; and thirdly, that there is no reason why connective tissue should not become muscular whenever and wherever the need for it may occur, without necessarily being a reversion to an ancestral arrangement. Into the merits and demerits of these objections I do not now propose to enter: I only wish to put my own hypothesis, with the facts on which it is based, before you.

We have noticed that in some animals the abdomino-humeralis passes both superficial and deep to the pectorals, and that some of its fibres may even pierce the pectoral, to be inserted with the fibres of that muscle. It is also a fact that in many mammals the hinder (caudal) fibres of the pectoral rise from the linea alba, a considerable distance behind the xiphisternum, and cover a good deal of the external oblique and rectus ventralis (abdominis). Further, it is known that the abdomino-humeral and pectoral muscles are supplied by the same nerve from the internal cord of the brachial plexus, while the obliques, rectus, and intercostals are supplied by intercostal nerves. All these facts make me regard the pectoral muscles as part of the panniculus; and although the theory sounds somewhat startling at first, when one

considers the embryology of the parts it does not appear so unlikely. It is admitted that the ventro-lateral muscles of the trunk are divided into four planes, of which the deepest is formed by the transversalis and triangularis sterni, the second by the internal oblique and internal intercostals, the third by the external oblique, the external intercostals, and, I have no hesitation in adding, the supracostalis; the fourth layer is the panniculus. It is further asserted that the panniculus, or most superficial layer, is a delamination from the third layer, after the three others have been formed. The mesial ventral mass of muscle does not show the division into layers so well; it consists of the rectus and its sheath. The pectoralis is usually regarded as a delamination from the surface of the third layer. I, on the other hand, prefer to regard it as part of the fourth or pannicular layer, itself a delamination of the third layer, so that what appears at first sight a revolutionary suggestion, becomes on examination a matter of very slight moment.

Digastric (Depressor mandibulæ).—The most important point to bear in mind, in considering this muscle, is that it is not always really digastric, but that, even when it appears monogastric, it has a double nerve supply. The anterior portion of the muscle is supplied by the fifth nerve, the posterior by the seventh. Our knowledge of the anatomy of the fish tells us that the muscles developed in the first or mandibular visceral arch are supplied by the fifth nerve, while those formed in the second or hyoid arch derive their nerves from the seventh. Nerve supply is not always to be relied upon in determining the homologies of muscles, but there is good reason to agree with Humphry in regarding the anterior belly of the digastric as a portion of the myotome belonging to the mandibular arch, of which the temporal, masseter, and pterygoids are part, and of looking upon the posterior belly as part of the myotome of the second arch, from which are also derived the stylo-hyoid and most of the facial muscles. The central tendon is a remnant of the connective-tissue interval or myocomma between the two myotomes.

In dissecting three Ornithorhynchi, I found a muscle running from the sub-hyoidean septum, outward and a little forward to the mandible, not far from the angle: it was supplied by the fifth nerve, and lay superficial to the mylo-hyoid muscle, of which it

appeared a delamination, and with which its fibres had nearly the same direction (fig. 7). In the same animal a single muscle runs from the long tubular external auditory meatus to the sub-hyoidean septum: it is supplied by the facial nerve, and probably corresponds to the combined stylo-hyoid and posterior belly of the digastric. From this I am inclined to think that the anterior belly is an older muscle than the posterior, or, in other words,

FIG. 7.—Throat muscles of *Ornithorhynchus*. *a.a'*, part of panniculus; *b*, anterior belly of digastric; *c*, posterior belly of digastric; *d*, mylo-hyoid; *e.e'*, part of panniculus.

that the anterior belly is differentiated from the mylo-hyoid layer before the posterior belly is split off from the stylo-hyoid. This possibly may be the reason why absence of the anterior belly of the digastric is very rare in man, but absence of the stylo-hyoid is fairly common.

Excluding the monotremes, the digastric muscles of mammals may, I think, be divided into three classes.

In the first class the anterior and posterior bellies are separated

by a considerable length of tendon (fig. 8); the posterior belly narrows into a rounded tendon, which passes forwards until it reaches the region of the hyoid bone, then it runs inwards ventral to the hyoid bone and meets its fellow of the opposite side, forming an arch with the convexity forwards; this arch is quite independent of the hyoid bone, and is only attached to it by connective tissue. The anterior bellies of the digastric spring from the convexity of the arch and extend forward to the mandible close to the symphysis, touching one another in the

5

FIG. 8.—Digastric of Flying Squirrel (*Pteromys*). (From the *Proceedings of the Zoological Society*.)

middle line of the neck. This kind of digastric is not confined to any one order. It is found in all squirrel-like rodents (sciuromorphic), as well as in many of the mouse-like tribe or myomorphic, but it is never seen in the porcupine-like (hystriomorphic) or hare-like (lagomorphic) groups. It is also found in many of the insectivora, and in most of the cynomorphous monkeys and anthropoid apes, such as the macaques, cercopithecii, black apes (cynopithecii), baboons (cynocephali), orangs, and chimpanzees.

The second division of the muscle we may describe as pseudo-

monogastric (fig. 9). In this the muscle at first sight seems to consist of only one belly, but a closer inspection will, in my experience, always show some indication of a central tendon, usually in the form of a few tendinous fibres on the surface, though these seldom extend into the interior of the muscle when it is cut across, and there is only a very slight constriction of the muscle in the middle. The anterior bellies are usually attached to the mandible midway between the symphysis and the angle, and, instead of being flat planes meeting in the mid line of the neck,

FIG. 9.—Digastric of Guinea-pig (*Cavia cobaya*), showing pseudo-monogastric type. *a*, digastric; *b*, mylo-hyoid; *c*, sterno-hyoid; *d*, masseter.

they are usually rounded and leave a considerable expanse of the mylo-hyoid exposed between them. As we have already noticed, the double nerve supply is always found. This kind of digastric is found in the porcupine-like (hystricomorphine) sub-order of rodents, in kangaroos, in all carnivora (fig. 10), and in the vesper-tilionine and pteropine bats. In the latter animals, which include the fruit bats and flying foxes, Macalister has drawn attention to an oblique intersection indicating the central tendon. The presence of this intersection I have verified.

The third kind of digastric is intermediate between the other

two. It is the typical digastric of man, and consists of anterior and posterior bellies connected by a definite central tendon, the anterior bellies failing to unite in the middle line of the neck, but usually reaching forward to near the symphysis. This variety of the muscle is found in most lemurs and many monkeys, especially the New World monkeys (platyrrhini), gibbons (hylobates), and many specimens of gorillas.

It is quite easy to find transitional stages between these three

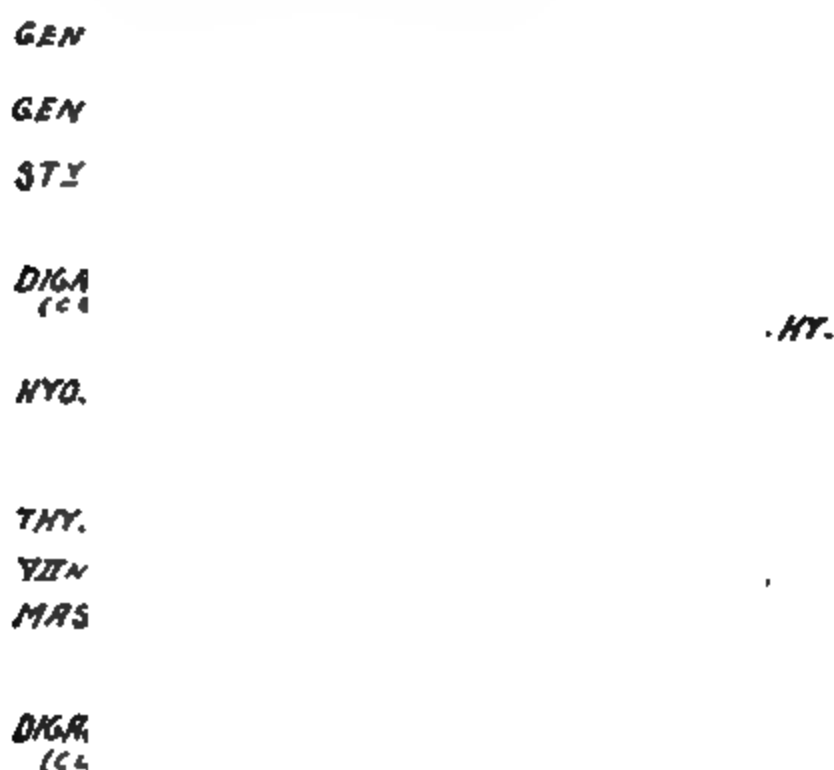


FIG. 10.—Throat muscles of Otter (*Lutra vulgaris*), showing cut digastric. (From the *Proceedings of the Zoological Society*.)

varieties of the muscle. We have already seen that some indication of a central tendon is almost always present, if carefully looked for, so that the second and third groups may easily pass into one another; while in many gibbons and semnopitheque monkeys the anterior bellies are connected by fibrous tissue across the middle line of the throat, and a little condensation of this tissue posteriorly would result in the definite sub-hyoid arch of the first variety. This arrangement I have recently seen in a spider monkey (*Ateles*). It is interesting to note that the commonest abnormalities of the digastric in man show transi-

tions from this third variety to the first or more generalised and primitive type; the anterior bellies are sometimes found meeting in the middle line; while Keith states that in a young human foetus the sub-hyoid arch may often be detected. The mento-hyoid muscle, which is found as an abnormality in man, running from the hyoid bone to the mental symphysis near the middle line, may be a remnant of the mesial part of the anterior belly of the digastric of the first variety; but about this muscle I have more to say later.

FIG. 11. — Digastric of Rabbit (*Lepus cuniculus*), showing absence of posterior belly. *a*, digastric; *b*, mylo-hyoid; *c*, genio-hyoid.

There are a few kinds of digastrics which will not fit into any of the above descriptions, and for these perhaps a fourth class should be established. They are true monogastric muscles, in which either the anterior or the posterior belly is suppressed. The lagomorphine or hare-like sub-order of rodents is a good example: here the posterior belly of the muscle is only represented by a narrow tendon (fig. 11). In many orangs it is curious that the anterior belly is wanting, and the posterior is attached to the mandible, close to its angle. In the mole (*Talpa europea*) the

posterior belly is normal, but close to the angle of the jaw the muscle narrows into a delicate tendon, which passes forward to be inserted into the body of the mandible about a third of the way back from the symphysis. I have been unable to find any other tendinous fibres or any nerve from the fifth, so I think that in this animal the anterior part of the muscle is absent.

I have not been able to think of any satisfactory explanation for one animal having one type of digastric and another a different one: it does not appear to be due to differences in the temporo-mandibular articulation. Dobson has suggested that animals which hold their food in their paws, and eat it with their heads flexed on their trunks, are the ones in which a sub-hyoid arch is found. This is a satisfactory explanation as far as rodents go, but there is probably no mammal which bends its head to take its food more than the fruit bat does, and yet this animal has an almost monogastric muscle, with no sub-hyoid arch at all. Again, why, among the primates, should the lemurs, spider monkeys, anthropoids, and man be losing their sub-hyoid arch? Probably we have not yet enough facts to try to find a satisfactory explanation.

The Ventral Group of Neck Muscles.—In this group are included the muscles which in man act as depressors of the hyoid bone, the sterno-hyoid, sterno-thyroid, omo-hyoid, and thyro-hyoid, as well as the continuation of these forward into the tongue. The group is usually regarded by anatomists as the prolongation forward of the rectus ventralis; and as the tongue develops in the floor of the mouth, some of this longitudinal layer becomes continued into it. The first thing that attracts attention in the abdominal part of the layer is the presence of tendinous intersections (*lineæ transversæ*), recalling the original myocommata and myotomes. In the cervical portion these inscriptions are seen in the central tendon of the omo-hyoid of man, and often in the sterno-hyoid and thyro-hyoid. The nerve-supply of the group is interesting. In man the tongue muscles are supplied by the hypoglossal and the depressors of the hyoid bone by the *ansa hypoglossi*. The hypoglossal nerve in some fish and amphibians is a spinal nerve which, higher up in the scale, becomes included in the cranium. It supplies myotomes behind those supplied by the seventh and ninth; and when these myotomes are prolonged into the tongue,

they carry their original nerve with them, consequently the tongue muscles are supplied by the hypoglossal; and in dissecting the submental region of the *Ornithorhynchus*, for example, we find the most superficial muscle supplied by the seventh nerve, because it is part of the facial panniculus, and is derived from the hyoid visceral arch; deep to this come the anterior belly of the digastric and the mylo-hyoid supplied by the fifth nerve, because they are muscles of the mandibular visceral arch; and deep to these, again, the tongue muscles supplied by the hypoglossal nerve (fig. 7).

Taking the question of the tendinous intersections, occasionally present in the sterno-hyoid and -thyroid of man, we find that they are constant in many mammals, but are more frequently found in the sterno-thyroid than in the sterno-hyoid. In a dog which I lately dissected, the sterno-hyoid and -thyroid were completely fused from their sternal origin as far as a tendinous intersection which was situated about a third of the way up the neck; after this they were separate. In a three-toed sloth (*Bradypus tri-dactylus*) the two muscles were fused as far forward as the cricoid cartilage, after which the sterno-hyoid was delaminated from the ventral and mesial part of the muscle as a slender slip to the hyoid bone. These specimens are interesting, because they bear out Testut's evidence, showing that the sterno-hyoid and -thyroid are mere delaminations of one muscular sheet. Tendinous intersections are found in many carnivora besides the dog,—in kangaroos, lemurs, and, according to Keith, in all cynomorphous monkeys; they are also common in the anthropomorpha. According to Chauveau, the tendinous intersection or myocomma is seen in its best development in the horse: here it is so large that the muscle is described as digastric, and the arrangement recalls that of my dog, in that the sterno-hyoid and -thyroid are only separable on the cephalic side of the intersection.

We have already noticed that the ventral layer of throat muscles is prolonged forward into the tongue on the dorsal side of the mylo-hyoid sheet: it is in many mammals prolonged forward ventral to this sheet as well. This has been noticed by Testut in the pangolin, armadillo, and anteater, and by Humphry in the hippopotamus, while Young found in three koalas some fibres of the omo-hyoid passing to the mandibular symphysis

ventral to the mylo-hyoid, while others passed deep to form the lingualis muscle. Windle found the sterno-hyoid continued forward ventral to the mylo-hyoid in the Australian rat (*Hydromys*); and I have recorded it in the coypu rat (*Myopotamus*) and the strand mole (*Bathyergus*). In the latter animal the muscle is continued forward as far as the symphysis menti. This arrangement never seems to occur in the primates, unless the mento-hyoid muscle already referred to may be regarded as the remains of a forward extension of the sterno- and omo-hyoid toward the symphysis. I do not know that the nerve supply of the mento-hyoid has ever been recorded; but if it comes from the fifth, the muscle is probably a dismemberment of the anterior

FIG. 12.—Tongue muscles of Macaque Monkey. *a*, hyoglossus; *b*, *b'*, basiglossus; *c*, stylo-glossus; *d*, genio-hyoglossus; *l*, tympanic bone; IX, glossopharyngeal nerve.

belly of the digastric; if from the hypoglossal, it is a remnant of the sterno-hyoid prolongation.

The *Hyo-glossus* muscle in man often consists of three parts. The main and most constant of these rises from the great cornu of the hyoid bone, and forms a continuation of the thyro-hyoid muscle towards the tongue. Nearer the mid-ventral line another set of fibres is sometimes found which rises from the lesser cornu of the hyoid, and is spoken of as the chondro-glossus; while less frequently a third bundle, called the triticeo-glossus, appears. This is situated more dorsally, and rises from the tip of the great cornu, or from the cartilago triticea in the lateral thyro-hyoid ligament. As far as I know, a separate chondro- or triticeo-glossus has not been recorded in the lower mammals, but I think that either the lemur or macaque monkey will give a clue to the meaning of the former muscle. In these animals the *hyo-glossus*

is sharply divided into two portions, the more ventral of which rises from the body of the hyoid bone, and perhaps slightly from the lesser cornu, while the more dorsal comes from the greater cornu (fig. 12). In the black ape (*Cynopithecus niger*) I found the ventral part of the muscle, which I believe corresponds to the chondro-glossus, still rising from the body of the hyoid, but overlapping the dorsal part above, as it does in man (fig. 13). In man the body of the hyoid is not as large as it is in the lower primates; and the chondro-glossus, when it is present, has to rise

FIG. 13. — Tongue muscles of Black Ape (*Cynopithecus*). *a*, hyo-glossus; *b*, basi-glossus; *c*, stylo-glossus; *d*, genio-hyo-glossus; *e*, thyro-hyoid; *f*, sterno-thyroid; *g*, crico-thyroid; *h*, thyroid gland; *j*, omo-hyoid; *k*, sterno-hyoid; *l*, hyoid bone; *m*, thyroid cartilage.

from the lesser cornu, so that what in the monkeys is a basi-glossus becomes in man a chondro-glossus.

The *Omo-hyoid*, as has been pointed out by Gegenbaur, is probably the lateral part of a large muscular sheet, of which the sterno-hyoid and -thyroid are the mesial portions. I have observed one or two points which support this theory. Among the porcupines the omo-hyoid is well developed in the climbing forms (*Sphingurus* and *Erethizon*), but in the ground forms (*Hystrix* and *Atherura*) it is usually absent. In one specimen of the ordinary porcupine (*Hystrix cristata*) I found the anterior (cephalic) portion of the muscle present as a very delicate layer, which, when it reached the deep surface of the sterno-mastoid,

gradually shaded off into the cervical fascia, instead of being continued on to the scapula. This, to my mind, is an evidence that the cervical fascia, or at all events that layer which passes deep to the sterno-mastoid, is the remains of a large fibro-muscular sheet, the mesial portion of which always contains muscular fibres as the sterno-hyoid and -thyroid, while the lateral part may or may not be muscular. Another evidence of the close relationship between the omo- and sterno-hyoid is the arrangement in *Bathyergus*, where the omo-hyoid is continued forward with the sterno-hyoid to the mandibular symphysis. Connecting-bands of muscle between the sterno-hyoid and omo-hyoid are recorded frequently in man: they also occur, according to Keith, in many monkeys, and I have seen one in a lemur.

The omo-hyoid, in the mammalia, appears and disappears with great freedom, and yet it is a good muscle for classificatory purposes, because it is fairly constant in animals nearly allied. It is present in monotremes and marsupials, in most ungulates, but not in *Procavia* (*Hyrax*), in all the myomorphine and sciuro-morphine rodents, sometimes in the hystricomorphine, but never in the lagomorphine; it is also present in the cetaceans and in carnivores belonging to the families of the ursidæ and mustelidæ, in most insectivora, in the cheiroptera, and in all the primates.¹ It is apparently absent in the edentates, though this order requires to have its myology worked up and collated, in many rodents as stated above, in most of the carnivora, with the exception of the two families named, and it is also absent in the families of the talpidæ, chrysochloridæ, and solenodontidæ of the insectivora. The study of this muscle in the mammalian series will give one a very good idea of how often the presence or absence of a muscle depends, not on the habits of its possessor, but on the position of that possessor in the animal scale. The ordinary digging mole (*Talpa*) has no omo-hyoid; neither has the aquatic desman (*Myogale*), which is closely related to it. On the other hand, the burrowing strand mole (*Bathyergus*), the arboreal dormouse (*Myoxus*), the aquatic vole (*Microtus*), and the leaping gerbille all possess omo-hyoids, because they are all myomorphine rodents. The presence or absence of an omo-hyoid

¹ I have lately found it wanting in the spider monkey (*Ateles*), but this may be an abnormality.

seems to be quite independent of the degree of development of the clavicle, since it is present in the non-clavicate ungulates, in potamogale, the only insectivore which has no clavicle, as well as in the cheiroptera and primates in which the clavicle is well developed.

The central tendon of the omo-hyoid is a structure which has given rise to a good deal of discussion. In by far the greater number of the lower mammals the muscle is riband-like and runs back from the hyoid to the anterior border of the scapula without forming a definite angle, the mesial border of the omo-hyoid lying close to the lateral border of the sterno-hyoid and -thyroid; it is only in the cheiroptera and primates that a constant fibrous intersection is present. Macalister has pointed out that in the ordinary insectivorous bats (*vespertilionidæ*) the muscle is slender and biventral, in the fruit bats (*pteropodidæ*) it has a very short central tendon, while in the vampires (*phyllostomatidæ*) the muscle is large and the intersection a mere streak. In the lemurs an intersection may or may not be present. Keith found it in the slow lemur, Mivart and Murie came across it once in nine specimens recorded, and I have seen it once in three lemurs which I have dissected.

Among the monkeys and apes there is a great deal of variability. The intersection is rare in the cynomorphous monkeys, while in the anthropomorpha it is much commoner, and in the chimpanzee is always present. Taking into account the late appearance of this intersection in the mammalian series, we are not surprised to find several recorded cases of human omo-hyoids in which it is entirely absent. The long intermediate tendon, which is so characteristic of man and many bats, must be due, I think, to the dorsal position of the scapulæ and the increased breadth of the shoulders. These tend to draw the more caudal part of the muscle away from its original line: the fibrous intersection would be more closely continuous with the surrounding fascia than the fleshy part, consequently that would be the point at which the bend in the muscle would occur. After the bend had been established there would be intermittent traction on the portion of fascia lying between the intersection and the proximal end of the clavicle, which would lead to its thickening, and eventually one would expect a pulley-like strap to be formed, as

is the case with the muscles in front of the ankle. This strap, by its pressure, would tend to convert the muscle adjacent to the

FIG. 14.—Shoulder muscles of Lemur. *a*, omo-trachelian; *b*, cleido-mastoid; *c*, sterno mastoid; *d*, trapezius; *e.e'.e''*, three parts of deltoid; *g*, *teres major*; *h*, *triceps*; *j*, *latissimus dorsi*.

intersection into fibrous tissue. This, of course, is a theoretical explanation of the formation of the central tendon of the omo-hyoid, the only fact at my disposal being that a central tendon

only occurs in animals with set-back scapulæ and broad shoulders. If the theory prove tenable in the light of fresh facts, it will harmonise existing views; for some regard the central tendon of the omo-hyoid as a myocomma between two myotomes, others as fibrous tissue produced by pressure. If the tendon were produced by pressure between the sterno-mastoid and scalenes, we should expect those muscles also to show some signs of it in the development of fibrous tissue where they are in contact with the omo-hyoid tendon.

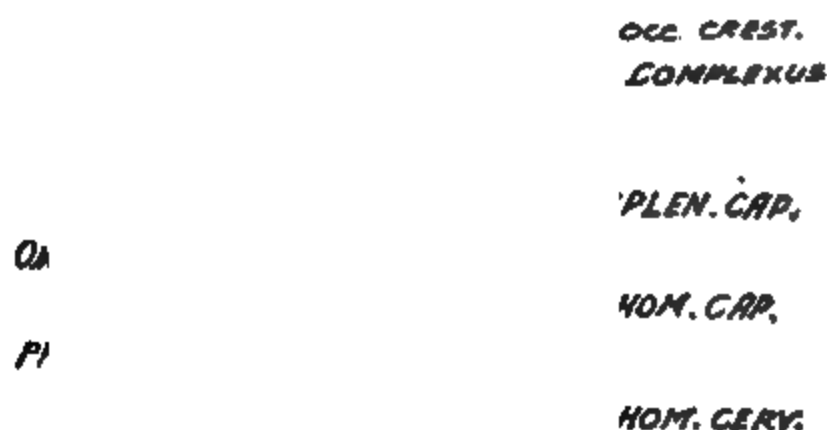


FIG. 15. Neck muscles of African Pole Cat (*Ictonyx*). (From the *Proceedings of the Zoological Society*.)

Omo-trachelian (*Levator claviculæ*).—This is a very constant muscle in mammals (fig. 14), but it only occurs as an abnormality in man. The most usual origin is from the transverse process of the atlas, but in certain animals (*e.g.*, hystricomorphine rodents) it rises from the basi-occipital bone dorsal to the attachment of the scalenus ventralis, which in these animals comes from here also. Its insertion into the acromion or, when it is present, the metacromion process is very constant, the only two exceptions with which I am familiar being the anthropoid apes and the bats. In these the muscle is inserted into the outer end of the clavicle, and I have little doubt that the change is due to the great

broadening and setting back of the shoulders in these animals. When the omo-trachelian occurs in man it has the same origin and insertion as in the anthropoids, rising from the atlas and sometimes the axis, and being inserted into the outer end of the clavicle. At its insertion the muscle is on the same plane as the trapezius, and, I think, should be regarded as part of the same sheet, which had to seek a deeper origin than the rest. It is always supplied by the 2nd, 3rd, or 4th cervical nerves. Its absence in man suggests that in the erect position it is no longer needed; possibly its chief function in the lower mammals is to fix the scapula for the long head of the triceps to act from in quadrupedal locomotion. This seems the more probable, in that the long head of the triceps is proportionately much smaller in man than in most other mammals.

Rhomboideus profundus.—This is another muscle which has often been described as a second or dorsal part of the omo-trachelian (fig. 15). It runs from the transverse process of the atlas to the vertebral end of the spine of the scapula, and is never, as far as I know, found as a distinct abnormality in man, but is possibly fused with the levator anguli scapulæ. Windle and I found it very constantly as a distinct muscle in the mustelidæ or weasel family of the carnivora, while in the other families it was either absent or blended with the levator anguli scapulæ or rhomboids. From its relations, we thought it must be a deep portion of the rhomboid plane. I mention it here as an evidence of the value of muscles for classificatory purposes.

(*To be continued.*)

A PRELIMINARY INVESTIGATION OF THE INFLUENCE OF BODY-POSTURE ON THE POSITION AND SHAPE OF ABDOMINAL AND THORACIC ORGANS.¹ By ARTHUR KEITH, M.D., F.R.C.S., *Senior Demonstrator of Anatomy, London Hospital Medical College.*

I. *The Object.*

THE object was to ascertain whether the form of the abdominal and thoracic viscera, as modelled by His, and as described by Symington, Cunningham, and Birmingham, and adopted in text-books, is true not only when the organs are fixed with the subject lying horizontally on its back, which was the position in which these observers fixed their subjects, but also holds true when the subject is hardened in other positions, as on the side or face, or upright on the head or feet. In other words, it was to see if organs like the liver and spleen retain the shape which we now consider normal, when the body is placed in different postures, or whether, to any extent, they assume a new form with each change of posture. It was found that they do change in shape as well as position, but many points have to be taken into consideration to determine the exact influence of body-posture on the shapes of organs.

II. *The Material.*

Altogether about 100 bodies have been preserved by the formalin method at the London Hospital Medical College, the subjects being injected as they lay on the back, and hence the organs were hardened and fixed in the position and shape they assume in a supine body. With the exception of observations made by Drs Sequeira and Leaf on the relationship of the liver and spleen to the surface of the body, which they will publish soon, no systematic record of these bodies was kept, but there was no overlooking the fact that there was an enormous

¹ Read at the February meeting of the Anatomical Society, 1898.

amount of individual variation in the shape and position of organs, and that the sexual difference was so great that a description applicable to man would not hold true for woman. In the series of bodies to which the present investigation applies, there were included:—

1.	Woman,	45 yrs.,	pleuritic adhesions,	.	.	hardened on back.
2.	„	65 yrs,	tub. and adh. of right lung	.	„	„
3.	„	65 yrs.,	no adhesions,	.	.	„
4.	Man,	70 yrs.,	no adhesions,	.	.	„
5.	„	68 yrs.,	{ old pleurisy of right lung }		.	„
			and sarcoma,		.	„
6.	„	65 yrs.,	no adhesions,	.	.	face.
7.	„	60 yrs.,	right lung solid and adherent,	.	„	„
8.	„	50 yrs.,	old pleurisy and pericarditis,	.	„	right side.
9.	Woman,	45 yrs.,	„	on right side,	.	„
10.	Man,	35 yrs.,	„	„	.	left side.
11.	Woman,	60 yrs.,	no adhesions,	.	.	„
12.	„	60 yrs.,	slight pleuritic adhesion,	.	vertical,	head down.
13.	„	55 yrs.,	no adhesions,	.	„	feet down.
14.	Man,	60 yrs.,	adhesion of right pleura,	.	„	„

Thus only 14 bodies were systematically examined, and individual variations being so numerous, the series is too small to afford ground for more than a mere preliminary statement.

III. *The Method.*

The body was placed on the injecting table, in whatever position it was desired to fix the organs, immediately on its delivery by the undertaker, and into a carotid or femoral artery, whichever the position made most convenient, was injected 5 litres of a formalin mixture (.1 formalin, .05 carbolic acid, .05 glycerine, .8 water). The body was thus preserved and its organs hardened. The body was allowed to lie for over three hours in the position in which it had been injected, in order that the organs might become completely fixed in the forms they then assumed. The body was kept in a tank until it was required in the dissecting-room.

Records were kept in the following manner. The body, when it reached the dissecting-room, was placed on its back; the table on which it lay was tilted up so that the subject assumed a partially upright position; a frame divided by wires into inch squares was placed over the body and an outline made, life size, on paper, also divided into inch squares. When the dissectors

exposed the sternum, ribs, crest of the ilium, etc., the body and frame were replaced in their former positions, and the parts exposed filled in the drawing. As the heart, liver, lungs, spleen, and kidneys were exposed they also were filled in, so that in the final drawing all the surface markings and organs of the body were shown in their relationships to each other, as seen from the front. The shape and surfaces of the organs noted were also kept after they were removed from the body.

IV. *Circumstances which render it difficult to say how far the Shape of Internal Organs depends on Body-posture, and which make it difficult to say how far the Changes observed in the Dead represent similar Alterations in the Living.*

The consistence of organs like the liver and spleen is softer and more plastic in bodies some time dead than in the living. Two surgeons of the London Hospital—Mr Dean and Mr J. Hutchinson, jun.—whom I consulted on the point were both positive as to the liver in life being a firmer organ than that seen in the post-mortem room, and therefore an organ that would change in shape to a greater extent. From some observations I made on the livers of dogs, a coagulation of the liver, not very marked, sets in after death, and disappears before the limbs lose their rigidity. In all the subjects included in this investigation *rigor mortis* had left the limb muscles, and it may be safely concluded had also left the viscera.

Yet one other circumstance prevents the application of facts ascertained from viscera of the dead to the living, namely, in life the blood pressure keeps the organs more or less distended and taut within their capsules; there is the same difference in rigidity between a living and dead organ as between a full and a partially full bladder.

Many circumstances increase the difficulty of determining the influence of body-posture on the shape of organs. Besides having to allow for a great sexual difference, and the state of distension of the stomach and colon, which Professor Symington has shown to be a powerful factor (*Edin. Med. Journ.*, Feb. 1888), for alterations caused by enlargements or adhesions, the results of disease, there still remains a great individual variation which

obscures the modifications in the shape of organs resulting from body-posture. Only the examination of a series four or five times as large as the one I have examined could eliminate individual inconstancies. Yet the position in which the subject is hardened undoubtedly is one factor in determining the position and shape of organs.

V. *The Viscera of the two Subjects hardened on the Left Side.*

The two subjects hardened on the left side showed more marked changes than any of the series examined. The posterior surface of the liver was reduced to a rounded border, the organ was greatly flattened, resembling the figures formerly given in text-books. It came in contact with the whole extent of the epigastric region of the abdominal wall, its lower border passing from the convexity of the 9th left costal cartilage to 2 inches below the convexity of the 10th right. The spleen, an organ of most inconstant shape, was flattened and oval, more so than is usually the case in bodies hardened in the supine position. In the woman's body the right ventricle was in complete apposition with the sternum and left cartilages, and so was over a third of the full extent of the left ventricle; in fact, the heart lay against the 7th, 8th, 9th, 10th ribs from the sternum to the anterior axillary line. In the man's body, the displacement to the left was not marked; perhaps an inch. It must be remembered that the arteries had been injected with plaster of Paris, and this is probably also a disturbing factor; but Professor Haycraft (*Journ. Physiol.*, vol. xix. pp. 496-506) found a very distinct displacement of the hearts of dogs hardened on their left sides compared with dogs hardened on their backs.

VI. *The Viscera of Subjects hardened on the Right Side.*

The organs resemble those of bodies hardened in the supine position, except that the liver is more distinctly triangular in shape, the right surface of the liver meeting at a prominent border with the upper surface. In both cases, the whole of the right auricle and part of the right ventricle lay to the right of the sternum. In the case of the woman, the spleen was triangular in shape, the base or the colic border being the longest,

while in the case of the man this organ was flat and oval, and lay completely in the costo-vertebral recess.

VII. *The Organs of Subjects hardened on the Face.*

In one case the liver was small and cirrhotic; the heart was displaced to the right to the extent of at least an inch, and descended behind the ensiform process for $1\frac{1}{4}$ inches. In this case, and also in the other, the right kidney was almost completely covered by the right lobe of the liver, and the spleen, which was triangular in shape, with a short colic border, was evidently displaced forwards.

VIII. *The Organs of the Body hardened in the Vertical Posture, Head down.*

The small bowel was drawn completely out of the pelvis, and the rectum, uterus, and ovaries exposed on opening the abdomen. The liver rose to the level of the lower border of the 3rd right costal cartilage, and its upper surface was dome-shaped, corresponding to the dome of the diaphragm. It was a woman's body, and yet the liver had almost completely receded within the costal margin. The displacement of the liver upwards on the right side had pushed the heart towards the left. The liver covered only half of the anterior surface of the right kidney. The spleen was flat and oval, resembling closely the model of that organ by His.

IX. *The Organs of Subjects hardened in a Vertical Position, Feet down.*

In the case of both the man and woman, the upper border of the liver corresponded to the lower border of the fifth rib; in the man it extended 1 inch below the right costal margin; in the woman $2\frac{1}{2}$ inches. The spleen in both cases was long and oval, but of prismatic shape, the three main surfaces being about equal in extent. In both cases about half of the anterior surface of the kidney was covered by the liver.

Only some of the more marked changes have been stated here. Excepting when the body is hardened on its left side, there appears to be no great alteration in shape of the organs; a

much larger series of bodies must be examined, and the results of the examination substantiated by clinical observations made on the living, to determine the minor changes caused by posture.

X. Points of some clinical interest that were observed.

It is possible that the greater area of heart that comes in contact with the chest wall when the patient is turned on his left side might be of some utility for the more accurate localisation, by auscultation, of cardiac lesions. The patient might be placed in such a posture between two pillows or beds.

If a description of the normal liver of the female were to be drawn from the bodies of this dissecting-room, it would be described as an organ extending on the right side to within an inch of the iliac crest, with behind it a wedge-shaped kidney, which has its thin apex above, its thick rounded base below, reaching to, or beyond, the iliac crest.

There is one point in connexion with the description of the spleen that ought to be noted, namely, that there are two quite distinct clinical areas on its diaphragmatic surface,—the anterior half, which lies beneath the ribs, and which can be marked out by percussion; the posterior half, which lies in the left dome of the diaphragm, and which cannot be marked out by percussioin.

In twelve of the fourteen bodies examined, the sigmoid flexure was on the surface, lying against the abdominal wall above Poupart's ligament of the left side. The vermiform appendix and the transverse colon did not occupy the same position in any two of the fourteen bodies.

There are one or two points in connexion with the stomach worth recording. If the body be injected before post-mortem relaxation of the walls of the alimentary canal has set in, the condition of systole or diastole of the gut, whichever state the bowel happens to be in at death, is preserved. Nearly always a constriction, sometimes obscure, at other times very well marked, divides the stomach into a very small pyloric part and a very large cardiac part. The constriction was present in six out of the fourteen bodies. In one woman a long, hour-glass constriction, corresponding to the constriction of the liver caused by tight-lacing, was present, so that one half of the stomach lay

above the waist, the other below. The stomach may descend to the umbilicus, as is seen in patients by special methods of examination, and yet not be enlarged. It is elongated, but what it gains in length it loses in width. As Treves found already, there was no regular disposition of the small bowel.

I must express my indebtedness to students of the London Hospital for the assistance they gave me.

**THE SHAPE AND POSITION OF THE BLADDER IN
THE CHILD. By A. BIRMINGHAM, M.D., *Professor of
Anatomy, Catholic University, Dublin.***

IN the year 1889, soon after the publication of Professor Symington's work on the Anatomy of the Child, I commenced an investigation into the shape and position of the child's bladder, by what I believe was then a new method. The difficulty of procuring suitable material was so great that after continuing the work for nearly two years, during which time only six bodies of a proper age were available, I finally suspended operations, in the hope of being able to carry my investigations to a more satisfactory termination at some future time, a hope which, so far, I regret to say, has not been fulfilled. However, as there seems at present to be no immediate prospect of suitable material coming into my possession, I have decided to publish a short account of the work so far as it has gone.

Although, in approaching the subject, I recognised fully the invaluable aid which the sectional method has given to anatomical research, still I felt that it was possible to overrate this aid, and to place too much reliance on its results, were they not checked by different methods. A frozen section shows perfectly the relations of a part or organ in any given plane, but much as to the general shape and surroundings remains to be made out by other means. In the bladder particularly this seemed to be the case. I consequently sought for some new method of examining this organ in the child, hoping thereby to be able to corroborate the results which Professor Symington had obtained by the sectional method, and, perhaps, to add somewhat to our knowledge of the organ.

After some consideration of the subject, I hit upon a plan which, it seemed to me, was likely to yield satisfactory results.

METHOD.

My idea was to inject the bladder to a state of natural distension with some material of about the same specific gravity as

urine, which would soon solidify, and which would be elastic enough to regain its shape if slightly disturbed. After injecting the bladder and allowing the injected material to set, the abdomen was to be opened, the level of peritoneal reflection observed, and a cast made of the bladder with the surrounding parts *in situ*. The bladder was then to be removed with as little disturbance of its shape as possible, having previously marked on it the level of the pelvic brim, and a cast of it also made. Finally, the injected organ, after removal and casting, was to be cut across at the level of the pelvic brim, and the amount of injection contained above and below the brim measured.

The first difficulty in carrying out this plan was the selection of a suitable injecting material. Plaster of Paris was first tried, and rejected, owing to its great weight, which produced decided distortion, and for other reasons. Finally, however, a solution of gelatine was considered the most satisfactory, and was accordingly selected. It is light, easily manipulated, it solidifies with sufficient rapidity, and it is possessed of a most important quality for such purposes as the present, namely, it is extremely elastic, and quickly regains its original shape when disturbed.

Another difficulty was the quantity to be injected. At first it was simply guessed by the amount of resistance offered to the syringe during injection, which was, of course, a very unsatisfactory method. Next, an attempt was made to inject with the aid of a bent tube to a measured pressure of so many inches of jelly, but owing to the viscid nature of the injection, this was found impracticable with the very narrow tubes which could be fitted into the small urethra of a child. At length a plan was devised which removed this difficulty. The bladder was first emptied as completely as possible with a catheter, then one limb of a glass tube, which was bent at right angles, was introduced into the urethra, and water poured through it into the bladder, until finally it stood at a given pressure, say 6 inches, in the vertical limb of the tube outside the urethra. The water was then drawn off and measured, and a quantity of jelly exactly equal to the water drawn off was introduced into the bladder, either with a syringe or through the tube. Unfortunately I was unable to find any table of the normal pressure within the distended bladder of the child at different ages. In fact, the

only information I could obtain on the subject of the intravesical pressure was the well-known statement, found in most physiological text-books, that, with the spinal cord intact, the bladder (of the adult) can withstand a pressure of twenty inches of water, but when the connexions with the cord are severed, it is capable of withstanding a pressure of only six inches. From these slender data I had to form my conclusions as to what the pressure might be in the child at various ages. After making a few injections under a fixed and predetermined pressure, I observed certain facts in connexion with the injection which seemed to afford a simple and satisfactory method of determining the normal full distension of any particular bladder.

I found, on injecting the water, that up to a certain point fluid flowed freely into the bladder, even with a very small pressure in the vertical limb of the tube, and that every slight increase in pressure was immediately responded to by the entrance of more fluid. When, however, this critical point was reached, even a considerable increase in the pressure caused comparatively little more fluid to enter the organ. This point, it appeared to me, indicated the full normal distension of the bladder.

Having injected the bladder, first with water and then with jelly, in the method just described, the body was placed on its back on a sloping surface, and set aside to allow the jelly to solidify. When sufficient time had elapsed for this to take place, the abdomen was opened in the following way:—A vertical incision was made on each side, from the thorax to pelvis, about $\frac{3}{4}$ inch from the middle line. This went at once through all the layers of the abdominal wall. Transverse cuts were also made on either side. There remained, when the cavity had been thus exposed, a median band of the anterior abdominal wall extending from thorax to pubes; on the back of this, the level of peritoneal reflection was carefully noted. The band was then cut, and reflected up and down. A long, sharp pin was now driven through the symphysis pubis and through the bladder until the point was lodged in the sacrum posteriorly—this is to prevent any movement of the organ. The sacro-vertebral angle and the upper margin of the symphysis pubis having been carefully defined, two small pins were inserted into the bladder, on the back and front, exactly opposite these points. In this way the level of the pelvic

brim was distinctly marked on the bladder. Then—the intestines, with the exception of the sigmoid flexure and the rectum, having been cautiously removed in some specimens, whilst in others they remained undisturbed—a cast of the abdomen was made, which showed the position and relations of the bladder and the surrounding structures *in situ*.

Next, the bladder was removed, great care being taken that its shape was not altered in this process,—a matter which, owing to the elastic nature of the injecting material used, gave rise to no great difficulty. A thin twine was fixed around it at the level of the pelvic brim, as indicated by the small pins previously inserted, and a cast of the organ thus prepared was made. This cast showed the size and shape of the bladder; and the encircling twine, which in the cast appeared as a slightly elevated ridge, indicated the line along which the plane of the pelvic brim intersected the bladder, and showed at a glance how much of the organ lay in the pelvis and abdomen respectively.

Finally, after the cast of the bladder had been made, the injected organ was cut across along the twine, that is, along a plane corresponding to the brim of the pelvis, and the jelly in each resulting part was melted separately and measured. This gave exactly the amount of the contents of the injected bladder which lay above and below the pelvic brim respectively.

RESULTS.

I shall here detail briefly the chief points concerning each of the specimens, and then state the conclusions to which I have come from an examination of the series. Unfortunately, two of the bladders—those of a one day, and of a nine months old child—got injured during or after removal, consequently casts of these are wanting.

No. 1. *Male Child one day old*.—Urine drained off by catheter, jelly injected, amount of injection judged by resistance offered. (In passing, it may be remarked here, that as a rule, in males, I slit open the urethra along its ventral aspect fully down to the base of the penis, in order to facilitate the introduction of the injection.)

In this case the distension of the bladder seems to have been complete,—possibly excessive. The abdomen was opened in the manner described above; the reflection of the peritoneum from the

bladder on to the anterior abdominal wall was found to be at a point midway between the umbilicus and the top of the pubes. Casts having been made, as already described, the bladder was cut across at the level of the pelvic brim, and the contents of each division measured. The part within the pelvis contained 4 drms., the part in the abdomen 4 drms. 5 mins.

On looking at the cast of the abdomen, one is struck by the marked projection of the bladder into the abdominal cavity; and from an inspection of this specimen, it can easily be understood how it became the custom to describe the bladder in the child as almost entirely an abdominal organ. But this abdominal position of the viscus is to some extent apparent rather than real, as the following considerations will show:—(1) If the cast of the removed bladder alone be examined, it will be seen that although there is so large a portion of it in the abdomen, still much more than would be imagined from viewing the open abdomen lies within the pelvis. (2) On measuring the contents, it is seen that the amount above the pelvis exceeds the amount within it by only 5 minims. (3) In the infant the pelvis seems, as it were, to project into the abdominal cavity proper, probably on account of the slightly developed lumbar curve, and the small development of the lower, or pelvic, as compared with the upper part of the abdomen. (4) The bladder *seems* to project out of the pelvis more than is really the case, on account of the small size of the pelvis relatively to that of the bladder at this time of life. But, as shown, even at the early age of one day, almost equal parts of the bladder lie above and below the level of the pelvic brim.

In shape this bladder is a somewhat elongated ovoid, slightly flattened from above downward in its pelvic portion. The abdominal is a little larger than the pelvic end or base, which latter does not project posteriorly, even to the faintest degree, behind the attachment of the diminutive prostate; in fact, a vertical line let fall from the most prominent part of the organ would cut the posterior part of the prostate.

No. 2. *Male Child one day old.*—The bladder was injected to what was judged, by the resistance and by measurements previously made, to be slight distension. The blood-vessels were also injected from the thorax, and the other steps described above carried out.

The peritoneal reflection took place one-eighth of an inch above the mid-point between pubes and umbilicus. Some time elapsed after the injecting, before the bladder was removed, with the result that it was unfit for casting.

The cast of this abdomen and of specimen No. 1 show well the large triangular surface of the child's bladder, bounded at each side by the hypogastric artery, with the base at the pubes, and the apex at the urachus, which lies in direct contact with the abdominal wall, without the interposition of peritoneum.

No. 3. *Male aged nine months.*—Jelly was injected in the method described until a pressure equal to 6 inches of water was reached. On opening the abdomen the peritoneal reflection was found to be situated at a point 1 line below the junction of the lower and middle thirds of the distance from umbilicus to pubes. The abdomen was cast, the bladder removed, and a mould of it secured, which unfortunately was broken before a cast had been obtained. A cast of the removed bladder of this child is therefore wanting in the series. The abdomen shows the gradual sinking of the bladder into the pelvis as the age advances: it is neither absolutely nor relatively so prominent as the bladder in the child at birth. The abdominal end was larger than the part situated in the pelvis.

No. 4. *Male Child of four years—very small for this age.*—The bladder was injected to a pressure of 8 inches of water. The peritoneal reflection took place at a point half way between the pubes and the umbilicus. Casts having been made, the bladder was divided, and the contents of its two parts measured. In the pelvis were 2 oz. 2 drms., above the pelvis 1 oz. 4 drms. 50 mins., making a total capacity of 3 oz. 6 drms. 50 mins.—not an excessive amount, in view of the fact that a child of four years may pass over $4\frac{1}{2}$ ounces at one micturition. However, as pointed out above, this child was remarkably small for his age.

The cast of the bladder, which was certainly quite full—if not perhaps over-distended—is egg-shaped, flattened somewhat from above downwards, the wide end of the ovoid being directed forward and upward, the narrower end backward and downward. This latter end projects to a moderate extent behind the plane of the prostate.

In this case, instead of being a true ovoid, the bladder seems to be made up of halves of two unequal ovoids, joined about the brim of the pelvis. The smaller half occupied the pelvis, the larger projected into the abdomen.

No. 5. *Male aged six months—a large child.*—Bladder injected with jelly to a pressure of 6 inches. The peritoneal reflection was at the junction of the lower and middle thirds of the distance between the umbilicus and pubes. Casts of the abdomen and bladder having been made, the bladder was removed and divided. The pelvic portion contained 1 oz. 40 mins., the abdominal portion 1 oz. 3 drms.

The cast of the bladder, although of large size, shows, by the large amount which projected out of the pelvis, that it belonged to a young child. The shape is that of an elongated and slightly asymmetrical ovoid, with a wide end directed forward and upward, and a narrow end looking in the opposite direction. This end projects slightly behind the plane of the prostate and urethra.

No. 6. *Male aged two years.*—In this case the bladder was first emptied of urine, and injected with water to a pressure of 3 inches, at which pressure 2 oz. 1 dr. 10 mins. entered; the pressure was then increased to 8 ins., when only an additional $1\frac{1}{2}$ drms. entered; 2 oz. 1 dr. 10 mins. of jelly were then injected.

The peritoneal reflection was remarkably low, namely, only $\frac{1}{4}$ inch above the pubes, the distance from pubes to umbilicus being $2\frac{1}{2}$ inches. Casts having been made, the division of the bladder gave the following results.—in the pelvis, 1 oz. 5 drms.; above the pelvis, 4 drms. 10 mins. The cast of the abdomen shows at a glance that the bladder is not nearly so prominent in this case as in the younger subjects.

The cast of this bladder gives, I believe, a more correct idea of the shape of the moderately distended bladder of the child than any of the others of the series. The shape is ovoidal, the slightly larger end being directed forward and upward, the narrower end backward and downward. The outline is irregular, owing to the fact that the bladder had been impressed by the surrounding structures; and this is, I believe, the natural condition of the moderately distended organ.

CONCLUSIONS.

I. *As to the level of the peritoneal reflection from bladder to anterior abdominal wall.* It was as follows:—

In two children, each one day old: half way between pubes and umbilicus.

In a six months child: at the junction of the lower and middle thirds of the interval between pubes and umbilicus.

In a nine months child: at the same level as the preceding.

In a two years child: one-quarter inch above the symphysis, *i.e.*, one-tenth of the distance between pubes and umbilicus.

In a four years child: half way between the pubes and umbilicus; this with a very full bladder which would raise the level.

These facts speak for themselves: they show the high level at birth, the gradual descent, with the occasional irregularity.

II. *As regards the position of the bladder.*—The casts give a clear idea of the extent to which the bladder may be considered an abdominal organ in the child at various ages. It will be noticed that even at birth, when its projection into the abdomen proper is most marked, very little more than half of the organ projects out of the pelvis, and this even with a fully distended bladder; with less distension there would be relatively less of the bladder in the abdomen. On examining the casts at more advanced ages the gradual sinking into the pelvic cavity is observable without interruption, as we pass from the youngest to the oldest specimen.

The amount of jelly contained in the abdominal and pelvic portions of each bladder shows this even more strikingly. In four bladders from children of different ages, the amount above and below the pelvic brim was as follows:—

One day old: in pelvis, 4 drms.; in abdomen, 4 drms. 5 min.

Six months old: in pelvis, 1 oz. 40 mins.; in abdomen, 1 oz. 3 drms.

Two years old: in pelvis, 1 oz. 5 drms.; in abdomen, 4 drms. 10 mins.

Four years old: in pelvis, 2 oz. 2 drms.; in abdomen, 1 oz. 4 drms. 50 mins.

Notwithstanding all this, it must be admitted, on looking at

the cast of the child one day old, that the bladder in its general appearance is, at this age, very largely an abdominal organ.

III. *As to the shape of the child's bladder.*—The shape of the distended bladder within the body will be in great part determined by three factors, namely, (1) the pressure within the bladder; (2) the pressure exerted upon it by the surrounding structures; and (3) the absolute or intrinsic shape of the organ itself.

The intrinsic shape of the bladder in the child is, I believe, approximately that of an egg flattened somewhat from above downwards, with the slightly larger end directed upwards and forwards, and the smaller end lying downwards and backwards.¹

Its assumption of this shape in the body will depend on the pressure of its contents, as compared with the pressure in surrounding parts, particularly in the rectum. If the pressure in the rectum be greater than that in the bladder, the former will indent the latter, and thus disturb its symmetry. If, on the other hand, the pressure within the bladder be the greater, the rectum can produce but little effect upon its form, which will then approach nearer to a true ovoid. But this intravesical pressure—which is, of course, the result of distension, as a rule—is liable to produce asymmetry in another way. Owing to the position of the bladder—lying as it does partly in the diminutive pelvis of this age, partly in the more roomy abdomen—the pelvic portion is surrounded by resistant structures, and can expand with less freedom than the abdominal portion, which, to a large extent, is free from any such restraint. Consequently, when the bladder is fully distended, there is a tendency for the abdominal segment to undergo an enlargement out of proportion to that of the rest of the organ, with a resulting disturbance of symmetry.

The condition of the base of the bladder varies at different ages. In the child at birth it is very slightly developed, and runs upward from the posterior wall of the urethra, practically as a vertical surface, forming no bulging whatsoever posteriorly

¹ In a mesial frozen section through such a bladder, the abdominal might appear to be smaller than the pelvic end (although the reverse is really the case), owing to the flattening from above downwards affecting chiefly the abdominal portion. In other words, it is only by making sections in two different planes, by a reconstruction method, or by injecting the organ *in situ*, that the true shape can be realised.

over the prostate. At six months it projects very slightly backwards behind the plane of the posterior wall of the urethra. And at four years the projection is distinct, behind both prostate and urethra, though not great.

Finally, taking the average condition with moderate distension, the bladder of the child under four years of age may be described as being egg-shaped, somewhat flattened from above downward, with the slightly larger end directed forward and upward, and the base, which is only feebly developed, projecting backwards very little, or not at all, behind the posterior surface of the prostate.

NATURAL SELECTION, AS SHOWN IN THE TYPICAL
SPEED-SKATER. By R. TAIT MACKENZIE, B.A., M.D.,
*Demonstrator of Anatomy, Medical Examiner, and Instructor
in Gymnastics, McGill University, Montreal.* (WITH TWO
CHARTS.)

THERE is no occupation or business in modern life that illustrates better the law of natural selection than athletic sports, particularly those in which competitors are pitted, man against man, at strenuous contests of speed and strength ; in which every mechanical advantage in the insertion of tendons and the length of bony levers will count ; and where, out of hundreds of ambitious beginners, but very few survive to be ranked in the first class, and finally as champions.

Among the champions in any particular branch of athletics, there we would look for a development of that type of man who is best fitted for that form of effort.

In the recently published photos of Tom Cooper, a champion professional cyclist, in *Bearings*, p. 1154, we see this specialised development. Taking the upper and lower halves of the body, it is incredible that they belong to the same man, so small does the development of the back and shoulders appear in comparison with the magnificent thighs and legs.

Among the wrestlers we look for the enormous extensors of the neck and back, the magnificent torso and the rather short extremities, with long muscles and short tendons and elastic ligaments, insuring the joints against sprains. Among the bicyclists, we look for the deep chest and rounded back, poorly developed arms and shoulders, and enormous thighs and good calves. These peculiarities we find shown in photographs of champion riders,—as in the example of Cooper above cited.

There is no sport that shows this approach to a type both of bony framework and muscular development better than speed skating ; and here I hope to show the type that characterises all the best exponents of this form of athletics, which tests so well the qualities of speed and endurance.

In 1894 I had the opportunity of taking the measurements and

getting photographs of four of the best amateur and of several professional speed-skaters at the international skating races in February of that year. I also got further data on a similar occasion two years later; and in 1897 there were gathered in Montreal representative skaters from Norway, Germany, the United States, and Canada, for the World's Championship meeting, held on February 6th and 7th. Here there was opportunity of watching them at work and of making observations, the results of which are here set forth.

Perhaps a brief review of the action of the stroke may be of some assistance in explaining the peculiar development found so constantly in these athletes.

The position for all is practically the same. The back horizontal, with the head well extended, the object being to escape wind friction; the thighs flexed to at least a right angle; the arms lying folded across the back, except when spurting, when they are swung from side to side, usually with the elbow joint extended, and giving the illusion of flight in their long graceful sweep. In skating, the body moves from side to side; but in watching a skater approach, the head remains in the direct line, while the body only sways as the weight is transferred from one foot to the other.

The stroke may be said to begin at the head, which is first extended, then the back is held firmly by the action of the erector spinæ; the thigh is then abducted, rotated outward, and strongly extended, and the knee is powerfully extended as the push is given. The main force of the stroke is delivered with the foot flat on the ice, so that the soleus and gastrocnemii are used but little. The drive from the toe of the skate, which finishes the stroke and gives an outward swerve to the mark on the ice, is delivered after the main work has been done by the stronger muscle-groups of the thigh, buttock, and dorsum. The skates used by all the best men are about the same, having thin flat blades about 18 inches long, and with the heels slightly raised. These are screwed to the tightly-laced boots, and give a secure attachment to the foot.

The distances skated vary from 220 yards up to 10,000 metres; for in international contests the distances are usually reckoned in metres; and to be a world's amateur champion a man must

win three out of the four distances, and must compete and finish in them all, so that each champion must have both speed for the short races and endurance for the long.

The present holder of the professional championship of the world is J. Nilsson, an American of Swedish parentage. He has skated from childhood, and has taken little other exercise except swimming, cycling, and a little gymnastics. He has been competing in first-class meets for the last five years.

FIG. 1.

In fig. 1 we see the general characteristics of his figure: deep chest, poor arms, good back and buttocks, very well developed thighs, and indifferent legs.

The skating pose is well shown in fig. 2, which shows him spurting, and with arms down. Here the magnificently developed muscles of the thigh are beautifully shown, the long flat foot, and the strong loins. This is a very characteristic pose when making a final spurt just at the end of a race.

FIG. 2.

FIG. 3.

Fig. 3 shows John S. Johnson, who held the title till last year. He is also a swimmer and bicyclist. The apparent flatness of the chest is accounted for by a kyphosis brought on by bicycling; in fact, he is a good example of the bicycle stoop. This man has a chest expansion of seven inches. The smallness of the arms will be noticed, amounting almost to atrophy. The calf muscles measured one inch less than when he began skating three months before I saw him. The long thighs are strong and well supplied. The flatness of the foot is also very noticeable.

FIG. 4.

I will close these reports with one more example, that of J. K. McCulloch, the present amateur champion of the world (fig. 4). In his case the figure and development of the skater is masked, because in summer he is an oarsman and uses the paddle continually. He is a gymnast of no mean ability, and has been one of the mainstays of the Winnipeg hockey team, besides being a most successful bicycle racer. When the accompanying photograph was taken, however, he had been doing nothing but speed-skating for about four months, and the measurement of his calf had decreased about an inch and a half. His thigh is very long and the leg short, while the muscular development of the back, thighs, and buttocks is remarkable.

There seems to be in his case a special development of the tensor fasciæ femoris, well shown in fig. 5. His chest is round and deep. In nearly all cases the thorax is of the round barrel-shaped type, not, as a rule, admitting of very great mobility, but always very capacious. In runners this is the rule, while the broad and flat thorax is more characteristic of gymnasts and acrobats, jumpers and pole-vaulters, where skill and spasmodic effort is required rather than endurance.

The actual measurements of these men, and of two other

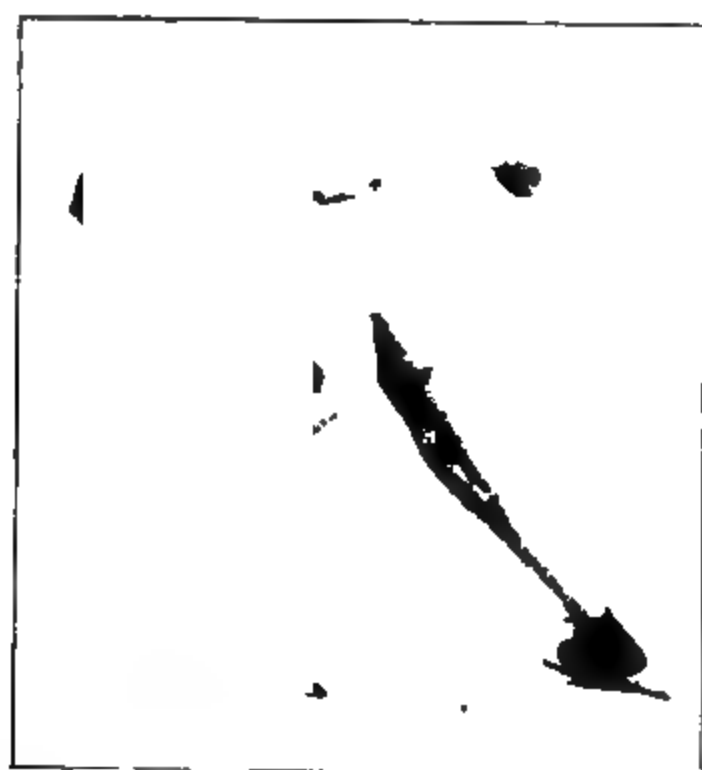


FIG. 5.

representative men, I have plotted on charts, that we may see graphically just where they differ from the average man.

The charts which accompany this are compiled from the measurement of 2300 Yale students, taken by Dr Jay W. Seaver. The double lines at the centre represent the figure at which the greatest number of measurements occurred, and hence indicate the mean rather than the average Yale student. The heavy figures are in the metric system, while the others are in pounds and inches and tenths.

In looking at the lines of chart I., which shows the measurements of the two present champions, amateur and professional, one is at once struck with their similarity: both of them are

surpassed in height by 75 per cent. of young men, but the length of their lower extremity up in the 60 and 65 per cent. class is made up largely of the long thighs. The next measurement of interest is the girth of the chest, which is low, except when inflated: the low chest-girth is accounted for by the poor pectorals, by the fact that they both have the rounded barrel-shaped deep chest, which does not get justice by the tape-line. After the girth of the hips, the lines diverge widely, showing M'Culloch's very high muscular development and Nillson's lack of the same, particularly in the arms. The lines approach at the thigh girths, which are above average in spite of their great length.

M'Culloch's large calves, from hockey, cycling, and foot-racing, here show in contrast with the smaller calf of the skater only. The breadth of the neck and shoulders also show this divergence, which is much less in the chest breadth.

In both, the abnormally deep chest brings them to the 100 per cent. line, and the small waist of M'Culloch again shows in the depth of abdomen. Both have large lung capacity, or rather chest mobility, as tested by the spirometer.

To sum up the main points of these two figures, we see that while they are below the average in total height (25 per cent.), and knee height (5 to 25 per cent.), they are up in the 60 and 70 per cent. class in length of thigh. While both are below the average in chest-girth (25 per cent.), they can expand to about the 75 per cent. mark; both have rather small waists (45 per cent.). In both the waist is narrow, and chest is broad and very deep.

I have taken the measurements of three slightly taller and older men on Chart II. J. S. Johnson has already been referred to. Adolph Norsing, a Norwegian, is a good type of the pure skater, for he has done little else in athletics since childhood. He is a very fast man, particularly for short distances. Olaf Nortwedt is also a skater pure and simple, so that, except for Johnson, who is perhaps more noted as a cyclist even than as a skater, we have here three pure speed-skaters, all in the first rank. Looking at the chart, we see great similarity in height and weight. The height of pubes could not be seen in this chart; the sitting height is low in all, and the knee height is

high, showing that their height is composed largely of thigh and leg, with comparatively short body. The three tracings show a marked similarity in long bone lengths, and also showing long feet. In the normal girths of the neck and chest, they are closely alike. Johnson's expansion of 7 inches makes a divergence in the inflated chest measurement. The muscle measurements of the arms are all low, although the elbows are large, this being a bone-, rather than a muscle-measurement.

The thighs all being long, they have not a very large girth, and the left in every case is larger than the right. This is the leg that carries the weight in making the turns at the end of the course. The calf measure is small, except in Johnson's case, where it is fair. The insteps are large, showing a flattening of the arch. The breadth of neck is good, and so is the breadth of chest, while the depth of chest is very high in all.

Here we have three men presenting certain marked characteristics in common, of average height: they have very long lower extremities, particularly the thighs; the feet and insteps long and large; girths are all small, except the bony ones, which are fair, and the thighs, which are above the average. The neck and shoulders are broad, and the chest deep and capacious, but not very mobile, except in the case of No. 1.

These characteristics can be seen in all who have excelled in speed-skating, and are interesting as showing the natural selection that has gone on till now. The type that will be looked for in future champions would be somewhat as follows:—

The arms would be undersized (fig. 1–3), from being idly crossed on the back; the neck broad and well developed, from the constant extension (fig. 4) in looking forward and upward; the extensors of the spine, particularly in the lumbar region, would be very large and strong (as shown in fig. 5). The thorax would be round, not very mobile; the heart strong, and the pulse slow, and not easily made rapid by exertion. The body would be short, hips rather narrow; very long, well-developed thighs and buttocks, and small calves, from the inaction caused by the long skate, that keeps the foot flat on the ice. The foot will be long and the arch flat: probably this is due to the tight lacing of the foot to the skate, and the gradual stretching of the

ligaments from the continual strain on them in their fixed position.

Jos. F. Donahue won the world's championship in 1892 in Poland, and held it until 1895. He has engaged in no other sport except rowing, and may be fairly taken as the typical speed skater, both from the length of his bones and peculiarities of his musculature, notably in the relation of his thighs to his legs, and of his extremities to his trunk.

These peculiarities of structure and development will be found in the human machine best fitted for this form of work, but there remain those nervous elements which we call 'control' and 'pluck,' the psychical factor which sometimes upsets the best calculations built up on statistics, and which neither the tape can measure nor can the scales weigh.

2.

3.

Also the measures of Mr. John S.
2. Adol.
3. Olaf

ON THE ARTERIAL ARCHES AND GREAT VEINS IN THE FOETAL MARSUPIAL. By R. BROOM, M.D., B.Sc.

OWING to marsupials being born at a very early stage of development, and, as a consequence, the lungs being functional organs at an earlier period than in the Eutheria, and also to the more lowly organised condition of the group, it seemed probable that a study of the heart and blood-vessels might reveal some features of interest.

The material at my disposal consists of a practically complete series of *Trichosurus* embryos from 8·5 mm. in length upwards. The smaller specimens have been sectioned, and it is in these that I have examined the blood-vessels. I hope shortly to be able to give a moderately complete account of the development of the principal organs; but in the meantime, as the blood-vessels present some exceptionally interesting features, I have thought it better to describe the condition in a special paper.

My 8·5 mm. foetus is unfortunately damaged about the head, but the thoracic and abdominal viscera I have found to be in good condition. The heart is in a most interesting stage of development, neither the auricles nor the ventricles being as yet completely distinct from each other; while in the aortic bulb, for the greater part of its extent, the aorta and the common pulmonary artery are in free communication. A little above the plane of the middle of the auricles the pulmonary artery, on becoming distinct from the aorta, curves round behind the latter, and after running parallel to it for a short distance, passes further back, and leaves the common sheath. The ascending aorta, on passing up a little further, divides into three parts, the left division being about twice the size of each of the others. The middle part is continued up as the right common carotid, while the right division passes upwards and backwards, and then curves downwards, where it divides into the right vertebral and right subclavian. From near the point where the division into vertebral and subclavian takes place, the remains of the obliterated right aortic stem can be easily traced downwards to the point where it unites

with the left aorta near the level of the upper part of the auricles. The left division of the ascending common aorta passes up but a very short distance when it gives off the left common carotid, and it then arches backwards and downwards, and having given off the left subclavian and vertebral arteries, is continued downwards as the descending aorta.

The common pulmonary artery near the plane of the upper border of the right auricle gives off from its right side a small branch, which passes upwards and slightly towards the right side for a distance of .14 mm., when it curves sharply backwards and then passes downwards, becoming the right pulmonary artery. From a point near the upper end of the ascending part, and just in front of the sharp bend, a thread of cells can be traced upwards to the under part of the right aorta at a point near the middle of its backward passing arch. The left or main division of the pulmonary artery is continued up to near the level of the bend of the right pulmonary artery, when it gives off from its posterior side a small branch, which passes backwards and then sharply downwards as the left pulmonary artery. Having given off this branch, the main artery is continued up to join the arching left aorta, as the *left ductus arteriosus Botalli*.

If the condition of affairs on the two sides be compared, it will be seen that, apart from the greater size of the main vessel on the left side, there is almost a perfect symmetry. We have the common pulmonary artery dividing into a right and left part, which, as they ascend, bear exactly corresponding relations to the neighbouring structures. The left branch is continued to meet the left aorta as the left ductus arteriosus, while on the right side the small ascending branch is continued similarly to the right aorta by the little thread of cells above referred to, and which there is no doubt is the remains of the obliterated *right ductus arteriosus Botalli*. On practically the same plane on which the left branch gives off the left pulmonary artery, the right pulmonary artery leaves the ascending right branch and its continuation of cells, and passes backwards and downwards.

It is impossible to make an accurate reconstruction showing the vessels and their branches, as they are so close together that a view from any side leaves some of the branches hidden by the others. Fig. 1, however, represents a semi-diagrammatic view

from behind, and is only diagrammatic in that the vessels are supposed to be slightly pulled apart to admit of the pulmonary branches being better displayed. Fig. 2 represents a section a

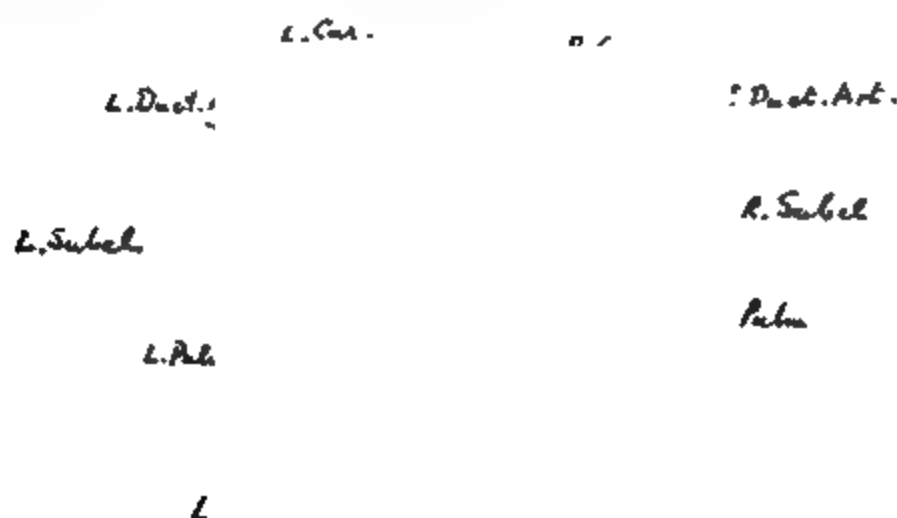


FIG. 1.—Arterial arches of foetal *Trichosurus*, 8.5 mm., from behind.

little above the division of the common pulmonary stem; and fig. 3 a section a little higher, through the right and left ductus arteriosi.

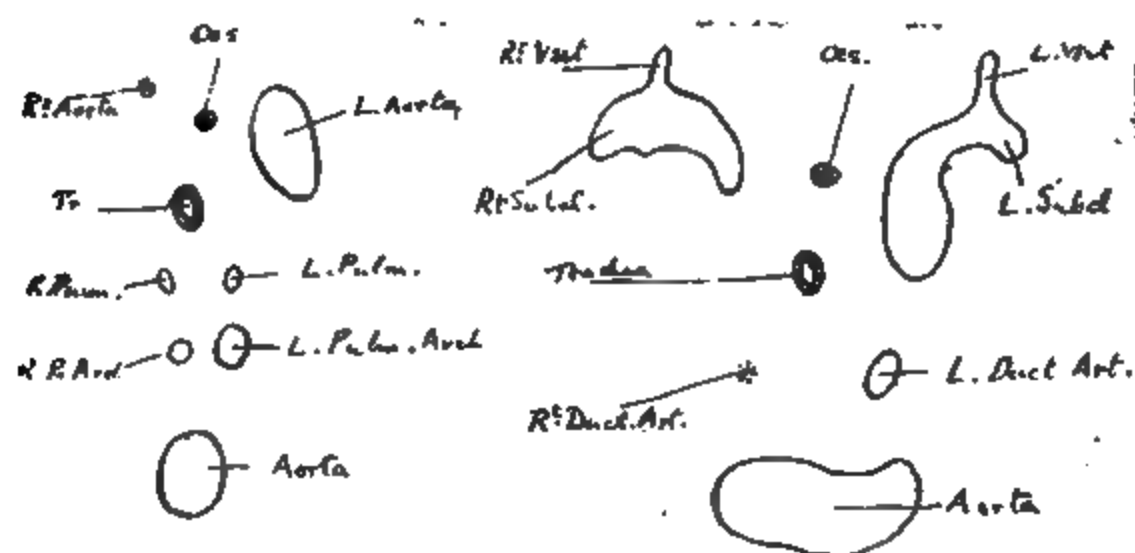


FIG. 2.

FIG. 3.

Hitherto, as believed by Rathke, the mammalian pulmonary arteries have been described as both arising from the fifth left arterial arch, although, both in reptiles and birds, the

pulmonary arteries arise from the fifth branchial arch of each side. It will thus be seen that the marsupial condition agrees with that described as occurring in the Sauropsida, and not with that of the higher mammals. In the Eutheria, however, at a correspondingly early stage of development, the pulmonary arteries are so small and so close together that it is just possible a mistake may have been made in supposing that each of the pulmonary arteries arise from the left arch; but should Rathke's view be conclusively confirmed, the marsupial condition will be of special interest, as affording evidence of the reptilian affinities of the group.

In tracing the veins through a series of sections there is greater difficulty than with the arteries, as, unless they be filled, the walls are so thin that, except in the case of the large vessels, it is almost impossible to follow them.

The cardinal veins, which are small, pass up behind the upper part of the developing lungs, and, curving over their apices, fall into the large jugulars to form the ducts of Cuvier. I am unable to trace the cardinal veins beyond the apices of the Wolffian bodies; and if any of the return blood from the Wolffian bodies be conveyed by these veins, it must only be that from the extreme upper part, as almost all the venous blood from these bodies undoubtedly, at this stage at least, returns by the inferior vena cava.

On tracing the inferior vena cava downwards it is found to arise by the union of the two iliacs, which latter can be traced from the root of the tail. On passing upwards, the iliacs lie on the outer side of the developing kidneys (at this stage only represented by the ureters, whose upper parts present a tubular dilatation—the future pelvis of the kidney—surrounded by a well-marked condensation of mesoblast). At the lower part of the Wolffian bodies the iliacs lie along their posterior and outer sides, but on passing up a little distance they curve round behind the bodies and come to lie on the inner side. On reaching the level of the umbilicus the iliacs unite to form the inferior vena cava.

I have not observed anything remarkable about the portal or omphalo-mesenteric veins, but in the umbilical vein we have a most interesting condition, and one very dissimilar from that

described in the higher mammals. Though at the very onset of the allantoic circulation in the higher forms there are two umbilical veins, the right one disappears very early, apparently, according to *Quain's Anatomy*, about the fourth week. In the marsupial, however, there remains a well developed *right umbilical vein* to a very much later stage. In the *Trichosurus* foetus, 8.5 mm. in length, and which corresponds roughly in its general development, in my opinion, to a human embryo of about six weeks, the following condition is found. A single moderate-sized

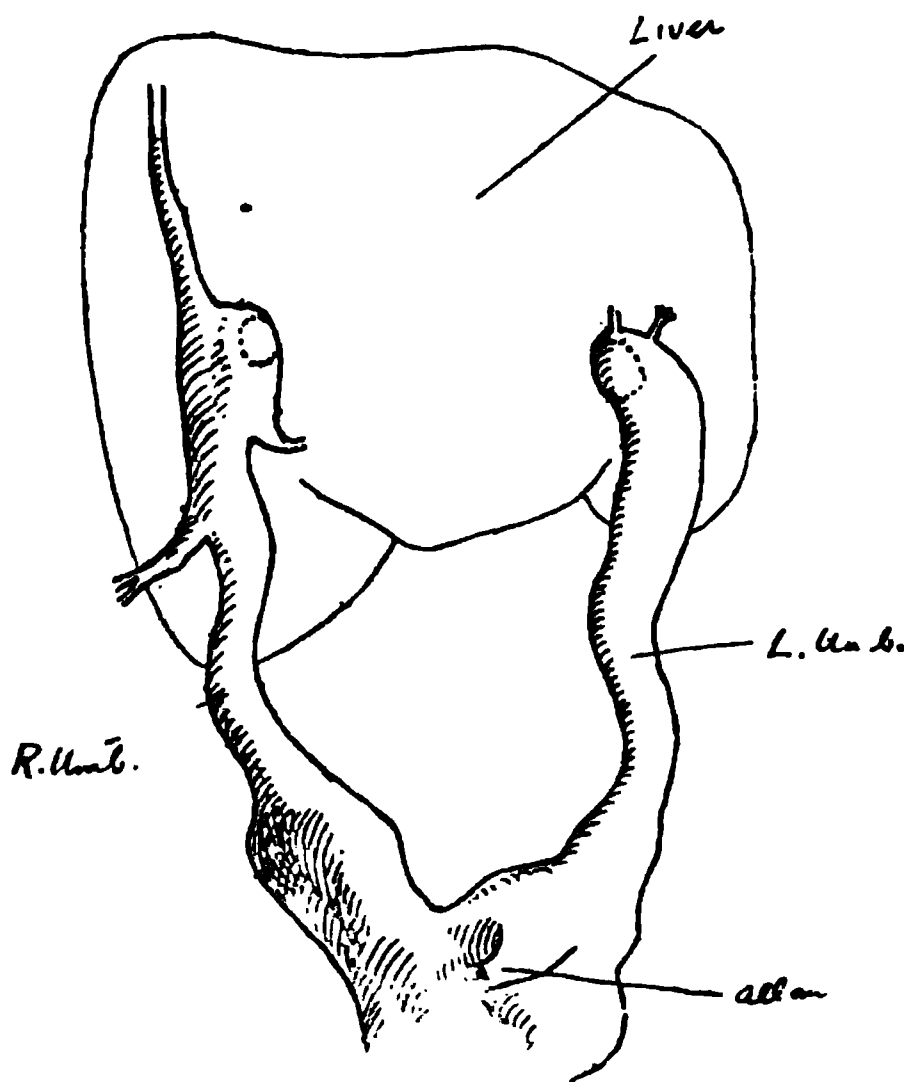


FIG. 4.—Umbilical veins in foetal *Trichosurus*, 8.5 mm.

vein brings back the blood from the allantoic circulation. On reaching the umbilicus it opens into a rather large sinus which lies round the lower margin of the umbilicus, and which is formed by the union here of the allantoic vein with the moderate-sized veins which pass up by the sides of the lower part of the front of the abdominal wall. From this 'umbilical sinus' there pass up to the liver two large veins, one on either side of the large umbilicus. The left vein, which is moderately uniform in size, runs up from the sinus a distance of 1.4 mm., and discharges into the liver in a situation corresponding to that in which the

umbilical vein opens into the liver in the higher mammal. The right vein is more irregular in size, and differs from the left in receiving in its course two moderately large branches from the abdominal wall, one on its outer side and one descending and falling into a sort of sinus just where the vein opens into the liver. A third small branch from the anterior abdominal wall joins the small superior sinus.

Figure 4 represents an anterior view of the umbilical veins and sinus, reconstructed from sections. The irregularity in the contour of the veins, especially the right, may be due, in some degree, to accidental pressure during and after death on the thin-walled vessels, but I have thought it best to illustrate the irregularities as they occur in the specimen examined. At this stage of development the whole body-wall, from the umbilicus to the clavicle, is imperfectly formed, being only composed of connective tissue—the ribs, sternum, pectoral and rectus muscles, though either formed or in process of formation, only as yet reach the most lateral parts of the front wall—so that in the abdominal region the recti abdominis muscles, of which only the rudimentary beginnings can be detected, run well outside and behind both the right and the left umbilical veins.

At its upper part the right vein opens into the liver through a rounded opening in the upper and anterior corner of the little sinus above referred to, almost exactly as does the left vein, and in a situation almost immediately above the developing gall-bladder. It will thus be seen that the left vein opens on the left side and the right on the right side of the quadrate lobe of the liver.

Each vein, on entering the liver through a small opening in its wall, falls into a comparatively large venous space. The tracing of the veins in the liver at this stage is a matter of considerable difficulty; but there is little doubt that each intra-hepatic venous sac gives off a small branch inwards and slightly downwards to the portal vein, and divides above into a large number of branches, which spread over the periphery of the upper part of the liver, and then pass inwards to fall into the inferior vena cava.

In a *Trichosurus* embryo of 10.5 mm. the umbilical sinus, though very much reduced, can still be detected. The develop-

ment of the sides of the abdominal wall has brought both the right and left veins much nearer to the middle line, and a further interesting change has taken place in that the right vein has become much reduced, and no longer opens into the liver. It is now merely a small vein which brings some blood from the anterior abdominal wall into the umbilical sinus. The left vein, which now carries all the allantoic blood to the liver, runs only a little to the left of the middle line, though the recti muscles are still widely apart.

A little later all trace of the right vein disappears, and the left vein, though comparatively small, follows a course very similar to that of the umbilical vein in the higher mammals. At birth, of course, the circulation through the umbilical vein ceases.

It will be observed that this doubling of the umbilical vein is very dissimilar to the condition found in the higher mammal, and very similar to that found in the early lacertilian embryo.

The only other veins to which attention need be called are the pulmonary veins. The right and left veins, though small, can be easily traced as they pass round in front of the lower end of the trachea just where it divides. Here they unite, and pass into the left auricle at its lower, inner and posterior corner.

THE CORRELATED DISTRIBUTION OF ABDOMINAL
PORES AND NEPHROSTOMES IN FISHES. By
EDWARD J. BLES, B.Sc. Lond., King's College, Cambridge.

THE term "abdominal pore" has been used in so many different senses, and has been applied to so many and diverse kinds of aperture in the cloacal region of vertebrates which are no longer regarded as homologous in any way, that a new definition is rendered necessary. The definition offered here is intended to include everything which is homologous in the widest sense: it recognises no distinction between genetically homologous openings, and openings acquired in a similar position and by a similar process, but quite independently, within the different groups of vertebrates. There are at present no convincing reasons for regarding the abdominal pores of dipnoi, ganoids, teleosteans, and reptiles as being phylogenetically derived from the abdominal pores of elasmobranchs, or the pores of any one of these groups as derived from those of any other or from those of common ancestors. This question is open for future investigation, and answer may come from comparative embryology.

Abdominal pores are the external apertures, usually paired, found in many Anamnia and some Amniota in the cloacal region, affording a passage of communication from the abdominal cavity to the exterior. The integument surrounding the pores externally is invariably ectodermic in origin, usually proctodæal. Internally the pores lead into the body-cavity, or into passages—the peritoneal canals—communicating with the body-cavity.

Peritoneal canals may be defined as paired diverticula of the posterior end of the body-cavity which extend backward alongside of the cloaca, and either end blindly, or open through abdominal pores to the exterior. Passages which appear to correspond to this definition are perhaps not always diverticula of the body-cavity, but represent the separate lateral coelomic spaces which have not become continuous along the mid-dorsal and mid-ventral lines. In such cases the abdominal pore may

open directly into the body-cavity without the intervention of peritoneal canals.

In many elasmobranchs the abdominal pores are not placed directly on the surface of the cloacal wall or on the external surface of the body, but the openings are situated on the lining of paired depressions of the integument called *cloacal pouches*. Balfour has described the development of these pouches under the name "abdominal pockets" (Memorial Edition, vol. i. pp. 451-2). They are involutions of the epiblast on each side of the opening from the hind-gut into the proctodæal groove. In the adult elasmobranch the pouches lie either within the

FIG. 1.—Diagrammatic horizontal section through the axis of the cloacal papillæ and peritoneal canal of a Selachian. On the right the abdominal pore is apical. It may open at any point between this and A P; in which case the papilla is solid.

cloaca or just outside the lips of the cloaca on the ventral surface, and are always near the posterior end of the cloacal opening. The cæcal ends of the pouches are always directed forwards.

The mouth of the cloacal pouch (fig. 2, O) is not the abdominal pore: it is present in *Scyllium*, for instance, long before the abdominal wall is perforated. Many writers, however, have taken them for pores, and this has caused much misconception. In two recent laboratory manuals the same view has been taken in the case of the dogfish and the skate respectively.

Overhanging the cloacal pouches in many species of elasmobranchs there are what I will call *cloacal papillæ*, corresponding to what Bridge not very appropriately called "peritoneal papillæ."

These papillæ occur in the dogfish, *Scyllium canicula*, and are represented in a diagrammatic horizontal section in fig. 1. They are attached in front of the cloacal pouch, and the apex is directed backward. The papilla is traversed by a peritoneal canal, a diverticulum of the body-cavity which opens near the apex of the papilla through an abdominal pore into the cloacal pouch.

On the left-hand side of the figure I have indicated by dotted lines the course of the peritoneal canal when it opens into the cæcal end of the cloacal pouch. In such a case the papilla is simply the double fold of skin produced by the involution of the cloacal pit, as is seen in any species of *Batis*. It is the

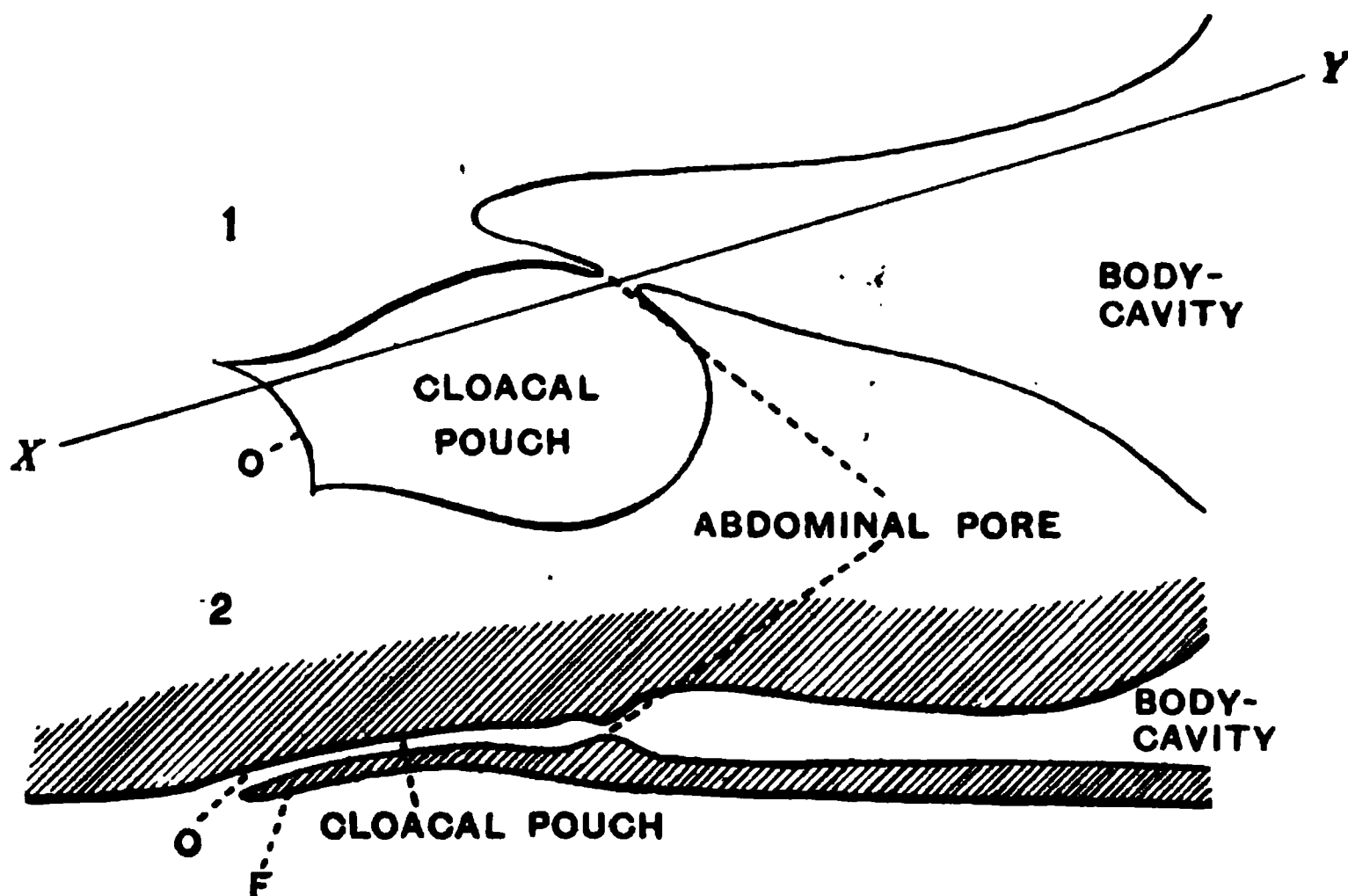


FIG. 2.—Diagram showing the relations of the body-cavity and abdominal pore to the cloacal pouch in *Raja*. 1, Parts of left side as seen from below X is the posterior end. 2, Vertical section along line X Y showing the marginal fold of skin, F, forming ventral wall of cloacal pouch. The edge of this fold is shown at 1, O.

fold of skin seen in section in fig. 2 (F) which forms the outer wall of the cloacal pouch, has become more or less separated from the body along the line of attachment (as shown in fig. 3), and has been pierced by the peritoneal canal. The greater the amount of detachment, the larger and longer will the papilla become, and the shallower the cloacal pit. This is actually the case in the series of species examined by Bridge and myself. Papillæ are large and well marked, while the cloacal

pits are small or absent, in *Carcharias glaucus*, *Galeus canis*, *Mustelus vulgaris*, *Triacis semifasciata*, *Pristiophorus cirratus*, *Scyllium stellare*, *Acanthias vulgaris*, and *Heptanchus cinereus*. Many of these cases are described below.

The interest attaching to this arrangement is, I think, chiefly physiological. If the abdominal pores are excretory openings, as I have reason to believe, they can serve as efferent channels only, not as afferent. There are, I believe, no sphincter muscles in connection with the pores, but the various arrangements described above form valvular contrivances, preventing the entrance of water into the body-cavity. If the pressure of the external medium be greater than the pressure inside the peritoneal canal and cloacal pouch shown in section in fig. 2, the total pressure

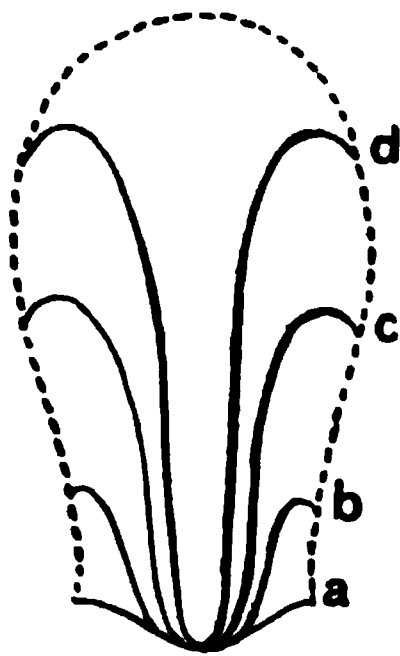


FIG. 3.—The dotted line indicates the outline of pouch; a corresponds to O in fig. 2, 1. The more this fold is detached along its edges, the more papilliform does it become, and the shallower the cloacal pit. In this way the cloacal papillæ have probably arisen from folds formed by the primitive invagination of the cloacal pouches.

on the flaccid outer wall of the pocket will be greater than the total pressure in the narrow slit-like opening to the pouch, and its lumen will become obliterated by the flap-like outer wall pressing inwards. When the pressure in the body-cavity is the greater, there will be a tendency for the canal, the pore, and the pouch to open. Thus, the flaccid peritoneal papillæ are compressed, and the lumen of the peritoneal canal closed by pressure from without, until overcome by a greater pressure from within. It is noteworthy, in connection with this, that the perforation of the papillæ is invariably on the side towards the cloacal pouch when it is not apical.

The anatomical evidence, then, seems to support the physio-

logical conclusions on the excretory function of the abdominal pores at which I arrived in a paper recently published on their distribution in adult vertebrates, showing that they alternate to a great extent with open nephrostomes in the adult, the reciprocal correlation being most clearly shown within the group of the Elasmobranchii.¹ There is also a well-marked alternation in the Amphibia and lower Reptilia when considered together, the Amphibia retaining open nephrostomes in the adult, and none possessing abdominal pores; the Chelonia and Crocodilia closing the nephrostomes during embryonic development, while many of them have peritoneal canals opening into the cloaca. In the present paper I shall deal with the relations of abdominal pores, peritoneal canals, cloacal pits, and papillæ in the Elasmobranchii, Holocephala, Ganoidei, Dipnoi, and Teleostei, and I shall present the anatomical evidence which throws light on the function of the passages from the body-cavity to the exterior. The distribution of the pores in the species of Elasmobranchs will also be dealt with.

A.—ELASMOBRANCHS POSSESSING NEPHROSTOMES WHEN ADULT.

1. *Species without Abdominal Pores.* (Fig. 4.)

Cestracion Philippi, Lacép.—Two small females (12" and 15" long) were examined by Bridge: they had cloacal papillae and pits, but "both . . . were quite imperforate." The specimens which came into my hands were likewise two females, one half-grown and one adult over 3 feet long. In neither of these were abdominal pores present: in fact, the larger specimen had a very much thicker abdominal wall than the smaller, in which the mercury in the body-cavity could be seen shining through the abdominal wall round the base of each cloacal papilla. The body-cavity of the large specimen nowhere came close to the surface, although it seemed to extend into the base of the papillæ, but the distal two-thirds of the papilla were quite solid. The abdominal wall in this region seems, therefore, to thicken in older specimens, and it would be extremely interesting to know whether abdominal pores are present at an immature age; and if so, whether their

¹ *Proc. Roy. Soc.*, vol. lxii., p. 232, 1898.

appearance and disappearance is correlated with any changes in the urogenital organs.

Rhina squatina, L., is the only other species which can at present be placed side by side with *C. Philippi*. I have, so far, only met with one case in which it appeared that abdominal pores were present in an individual of this species. A portion—the posterior part of the abdomen of a young monk-fish—is exhibited in the Hunterian Collection (No. 2677) of the Museum of the Royal College of Surgeons. In the catalogue, vol. iv. (1838), p. 135, the reference states: “At the sides of the external opening of the cloaca may be seen the peritoneal canals, through which white bristles are passed into the abdominal cavity. This certainly gives an appearance as though pores were present, but, as I have already insisted, the fact that bristles can be passed into the cloacal pits (here called peritoneal canals) to emerge in the abdominal cavity is far from being demonstrative of the existence of a pore: the body-wall is often so thin that it would offer no appreciable resistance to the passage of a bristle through it. There would be the less hesitation in so passing a bristle, since the openings of the cloacal pits were, by most of the older writers, and apparently also in this instance, regarded as the external apertures of peritoneal canals. So that, as late as 1880, Günther could assert (*Study of Fishes*, p. 123) that a paired porus abdominalis, one on each side of the vent, is found in all Chondropterygians. It is obvious that the conception of a cloacal pit into which an abdominal pore may or may not open was not entertained. The Hunterian specimen, then, is not admissible as evidence of the existence of pores in *R. squatina*. The whole of the valid information on the subject points to the absence of pores in members of the species which have not reached their full size. The five specimens (preserved in alcohol) which I have been able to examine ranged from 45 to 73 cm. in length: four were females and one a male. I can confidently state that these specimens were all without abdominal pores; in not one of them did mercury escape from the cloacal pits when the posterior part of the abdominal cavity was quite full of the metal. Indeed, in one of these specimens, a half-grown female, there was no trace of either cloacal pits or papillæ.¹ This

¹ In addition to these I have examined four fresh specimens, one male and

condition was found by Bridge on the left side in a female, which had a small papilla and very shallow cloacal pit on the right side. Both this specimen and a small male examined by Bridge were without pores. Quite recently (*Anat. Anz.*, vol. xiii. p. 393) Guido Schneider has made experiments on two specimens, one of each sex, of *R. squatina*, and has dealt with the alleged abdominal pores in them. In both specimens pores were present, but they were in part without a proper epithelial lining where they passed through the connective tissue, and hence were, in fact, ruptures of the abdominal wall at the point of least resistance. The part of Schneider's description which shows that this was the case, although the author himself does not seem to regard the openings as pathological, runs:—"Darauf folgte distalwärts eine Strecke von ungefähr o. 3 mm. Länge, die gar kein Epithel besitzt, wo also das perforirte Bindegewebe nackt zu Tage liegt. Das äusserste Zehntel des Kanals verläuft in der geschichteten Oberhaut, welche einfach durchbohrt ist und sich nicht in den Kanal hineinzieht. . . . Eine Verbindung zwischen der Oberhaut und der vom Peritoneum herstammenden Epithelauskleidung der Abdominalporen habe ich also nicht gefunden." The rupture of the body-wall in the position of the cloacal pits must be attributed to the injection, two days before the specimens were killed, of carmine and Indian ink into the body-cavity, and the peritonitis induced in consequence of the injection. As I have already had opportunity, in my earlier paper, of discussing Schneider's interesting results, I will at present only say that Schneider's observations support, if anything, those of Bridge and myself on the absence of pores in half-grown *R. squatina* in the normal condition.

The largest specimen of *R. squatina* which appears to have been searched for abdominal pores is a female 73 cm. long which I have examined; but as this fish is said to attain a length of 2 metres or more, this particular specimen was only half-grown, and it might perhaps be expected that the pores do not appear until maturity is reached. As remarked above, however, there is a tendency for the cloacal pits and papillæ to disappear in half-grown individuals; and this, I think, may be taken as an

three females, ranging from 71 to 83 cm. in length, in none of which were pores present.

indication that the pores will not be found in the mature fish, except perhaps as a pathological formation.

The nephrostomes are persistent, and seem to increase considerably in size as the animal grows. That they are functional has been proved by G. Schneider, as will be described later on.

2. *Species without Abdominal Pores until Full-grown* (Figs. 4 and 5).

The classification I adopted in Table II. (*l.c.*, p. 236) has one characteristic feature in common with most schemes of classification made to represent natural grouping of species. This feature is the difficulty arising when the division of the larger groups, one from another, is undertaken. The lines of demarcation must be more or less arbitrarily placed, and cannot be regarded with any confidence as representing actually existing divisions between natural groups until all of the species have been studied.

I have felt this difficulty especially in forming Group 2 in Table II. *Scyllium stellare*, L., and *Pristiurus melanostomus*, Bonap., have both persistent nephrostomes, and I had originally placed them with *Cestracion philippi* and *Rhina squatina*, on the strength of Bridge's observations, confirmed by my own. These two species are both included by Bridge amongst those without abdominal pores. He examined a large number of specimens of the *Scy. stellare* and three of *Pristiurus*; but he does not give the sizes of his specimens. In a male *Scy. stellare* 52 cm. long (spirit specimen), and in two male *P. melanostomus* (60 cm. and 65 cm. long), I found that the pores were absent, although both possessed cloacal papillæ. These were all mature individuals, but not of the full size reached by the two species. *Scy. stellare* attains a length of 1 metre and upwards, and *P. melanostomus* a length of 90 cm., according to Carus (*Prodrom. Faun. Med.*). When I examined a full-grown male of *S. stellare*, which was 95 cm. long, and had thus reached its limit of growth, I was surprised to find both large flap-like papillæ perforated by slits about 3 mm. long each, placed on the ab-axial side of the papilla. I have also examined a specimen (female) of *P. melanostomus* larger than the two spoken of above, and which was full-grown, 72 cm. long (in

spirit). On the right papilla there was a minute perforation, through which mercury escaped in tiny drops. There was no perforation of the left papilla.

The difference between these two Scylliidæ and those placed in the next group (3) consists, as far as can be judged at present, in the time of life at which the abdominal pores appear. *Scy. canicula* acquires them at about the period of sexual maturity, before the animal has grown to three-quarters of its full length. In Group 2 the pores are apparently not present until the full size of the species is very nearly reached, or they may remain closed throughout life.

3. *Species acquiring Abdominal Pores late (when sexually mature) or not at all.* (Figs. 4 and 5.)

Scyllium canicula.—A "large number of specimens" of this species were examined by Bridge, and he concluded that abdominal pores are absent. But, in a paper by Turner which accompanies Bridge's, it is stated:—"Behind the oviducts was a crescentic fold, such as Prof. Bridge has described as the crescentic septum. Posterior to that were two short papillæ, one on each side of the middle line. At the summit of each papilla was an orifice, into which a bristle could easily be passed into a funnel-shaped prolongation of the peritoneal cavity situated at the side of the rectum. These orifices were therefore true abdominal pores. At the base of each papilla, and situated more especially at its outer border, was a shallow pouch-like depression of the wall of the cloaca."

This description and Bridge's are in agreement, with the exception only of the perforation of the papillæ to form abdominal pores, and, with this exception also, my own observations confirm Bridge's account. The existence of open pores is likewise affirmed by Marshall and Hurst (*Practical Zoology*, p. 213, 4th ed.), with the qualification that they are often absent in young specimens, especially in females. The explanation of the apparent discrepancy is, I believe, to be found in the view that *S. canicula* is a species which varies in respect to this character. I have made a careful examination of eighteen specimens of dogfish, slitting the ventral abdominal wall as far as the

pelvic girdle, suspending the animal by the head and pouring mercury into the right and left posterior extremities of the body-cavity. Ten of the specimens had been preserved in chromic acid solution; and when no mercury escaped in these, I pushed a glass tube of suitable calibre down into the body-cavity until it was held by the peritoneal wall. By pouring into the upper end of this tube held vertically, a pressure of 10-12 inches of mercury was obtained. The mercury fills the hinder part of the body-cavity of that side only into which the tube is passed, and by distending the papilla of that side shows the extension of the body-cavity into the papilla itself. The abdominal pore is simply a perforation of the wall of the papilla, as into it the body-cavity is, in any case, prolonged. Of the ten hardened specimens only three possessed open abdominal pores, including one male with both open, one male with the left pore open and no right pore, and one small immature female with narrow oviducts and small oviducal glands, in which both pores were open. The seven individuals without pores included one male, three gravid females, and three adult females without eggs in the oviducts. Eight fresh dogfish were examined during the breeding season, four of each sex. One male was immature (22 ins. long) and without abdominal pores. The remaining three males and four females were all 25 inches in length, or longer, and all possessed open pores. Of the females, two were gravid and two had distended flaccid oviducts, and had probably deposited their ova. In one of the gravid females there was no right pore, resembling in this the male alluded to above.¹

It follows, then, that the absence of pores, as recorded by Bridge, and their presence in the adult, as described by Marshall and Hurst in *S. canicula*, are not irreconcilable results, inasmuch as a limited number of specimens might, on examination, prove either the one or the other to be correct. A larger number of specimens, however, when examined in a legitimate manner, without undue probing with bristles or seeker; will demonstrate

¹ It may here be remarked that amongst the elasmobranchs examined by Bridge, Turner, and myself, there are in all seven cases in which the pore on the left side only was present, two cases where the left pore was wider than the right, and only two cases where the right one was open and the left absent. There may be some connection between this asymmetry and the asymmetrical development of the ovary and of the kidneys (Howes, *Jour. of Anat. and Phys.*, xxiv. 407).

the fact that the occurrence of pores is quite inconstant, and is apparently arbitrary in its relation to sex or sexual condition, excepting that the pores, when present, do not open until about the period when sexual maturity is reached. The size of the orifice on the abdominal papillæ is never very great. The largest I have seen formed a slit 2 mm. long; as a rule, the pore was quite minute.

Spinax niger, Bonap., may, I believe, be placed side by side with *S. canicula*, at any rate provisionally, and until a larger number of specimens have been examined. Bridge found "well-marked, slit-like pores, but no distinct papillæ" in a male *S. niger*. I have only had three females of this species under observation. One of them was 14 inches long, and in it two pores, half a millimetre in diameter, were open close to and behind the posterior border of the cloacal opening. The pores had slightly tumid lips, but there were neither cloacal pits nor papillæ. A younger female (10½ inches long) was similar to this in all respects. But the third specimen, larger than either of these, and nearly 15 inches long, had no pores, although the body-cavity extended quite as far back as in the others, and the abdominal wall was extremely thin over the posterior end of the cavity on each side of the cloaca. As far as this somewhat scanty evidence goes, it appears that the pores are variable in their appearance in this species.

4. *Species which cannot, without further evidence, be placed in the above groups.*

It is uncertain to which of the above groups two other species of Spinacidæ belong, namely, *Centrina Salviani*, Risso, and *Centrophorus granulatus*, Blk. Schn. In an advanced embryo (17 cm. long) of *Centrina Salviani*, Semper found 23 pairs of open funnels; and as, where these funnels disappear, they do so very early in all other Plagiostomata, he believes that they will, therefore, be found to persist in the adult *Centrina*. The abdominal pores opened widely in the female examined by Calderwood. I have found a large female (38 inches) of *Centrophorus granulatus* from Madeira to have open segmental funnels, but not as many as Semper found in a male 40 cm. long. In his specimen there were 30, in

mine 17, but some of the anterior funnels may have been removed with the mesoarium, which, together with the ovaries, was wanting. The abdominal pores were simply perforations of the abdominal wall, forming slits 5 mm. long. In another female, which was only half-grown (18 inches long, from the Mediterranean), there were no pores, but in a still smaller one (from Madeira, 15 inches) the pores were long slits, as in the first. A male (14 inches) was without pores. There is sufficient irregularity in these data to make one hesitate to attribute, without further investigation, abdominal pores as a constant feature to the adults of this species.

Another species, in which abdominal pores exist side by side with nephrostomes, is *Hexanchus griseus*, Gm. Semper found the nephrostomes in a female 10 feet long, and I have been able to confirm his observations on a specimen 4 feet 9 inches long. In this young female the nephrostomes opened into the mesonephric tubules, as it was easy to see in transverse sections of the kidney. The abdominal pores were both open into the cloaca.

Heptanchus cinereus, Gm. Considering the morphological importance attaching to the anatomy of the Notidanidæ, I was glad to have an opportunity of examining a specimen of this species in the British Museum. There were open nephrostomes, like those described in *Hexanchus* by Semper. I counted seven pairs at least, but the conditions were not favourable for such minute investigation as is required, and there may be more which I did not see. Abdominal pores were present; they opened on short papillæ, and were slits 3 mm. long. There was no trace of cloacal pits. This individual was a female of small size, only 3 feet in length, and therefore scarcely half-grown. The single specimen examined by Bridge was also a female; he gives no data regarding size or age. The peritoneal papillæ were swollen and bag-like, but injection failed to demonstrate the existence of any pores by which their cavities could communicate with the exterior."

Open segmental funnels and abdominal perforations do then occur together in the same individual in *Centrina Salviani*, *Centrophorus granulosus*, *Heptanchus cinereus*, and *Hexanchus griseus*; but these cannot at present be classed in any of the four groups of Series A: a number of the adults of each species must

be examined to determine whether the occurrence of pores at that stage is constant or not. It is not certain that *C. Salviani* and *H. cinereus* retain open nephrostomes when quite full-grown, although that they do so can very safely be inferred. None of the Notidanidæ, in which the abdominal pores have been investigated, were, as far as I know, full-grown; and it would be very interesting to know whether the pores in such specimens (10 to 11 feet long) are open or not.

B.—SPECIES WITHOUT NEPHROSTOMES WHEN ADULT, AND ALL POSSESSING ABDOMINAL PORES. (Fig. 6.)

(2) *Raia maculata*, Mont., according to Bridge, has no abdominal pores, and, like the rest of the Batoidei, it has no nephrostomes. In combining both negative characters, this species would form the sole exception amongst the thirty-six species of Elasmobranchs in which both of these points have been investigated. Hence it was important that Bridge's observations should be confirmed. I therefore examined the British Museum specimens of this species, and found that in two full-grown male specimens a pore was open on one side and the other was closed—in one specimen the right, and in the other the left pore. This was determined by pouring mercury into the body-cavity. Applying this method to two female specimens in the same collection, I found that no mercury ran out at the 'cloacal pits'; but as both of these, one half-grown and the other a large individual, were extremely hard and shrunken in the cloacal region, I cannot be certain that the mercury reached the posterior end of the body-cavity, where the internal opening of the pore is placed.

In addition to these preserved specimens, I have also examined two males and one female in the fresh condition. The female and one male were young (18 inches and 22½ inches long respectively); both had abdominal pores. The other male was at least half-grown (3 feet 2 inches long), and it also possessed pores. When the presence of pores is ascertained by the passage of mercury through them, their position can easily be determined by dissection. The mercury escapes externally from below the lips of the cloacal pouches, which are sacs, opening just behind the cloaca, close to the middle line, and extending on each side as

far forwards as the middle of the longitudinal slit-like opening of the cloaca. They lie close below the integument, so that the ventral wall is formed by a flaccid fold of skin, which contains a little connective tissue and some small blood-vessels. The posterior free edge of this fold forms the lip of the cloacal pit. The lumen of the sac is generally occluded by the ventral external flap being pressed against the dorsal wall of the sac. By slitting up the pit along its outer margin, and turning the flap thus formed inwards towards the middle line, the pore can be seen on the median edge of the pouch as a slit about 2 mm. long, with slightly thickened lips; but if the depth of the pouch is divided into three equal parts, the pore is always placed within the middle third. A seeker passed into the pit will therefore, if pushed straight forwards, meet the blind anterior end of the sac. The pore leads directly into the abdominal cavity, no duct intervening. In the region of the rectum and cloaca, the perivisceral space retains throughout life its embryonic condition of separation into two lateral cavities, which are continued back almost to the level of the external opening of the cloacal pit, and lie alongside of the cloacal slit, just below the surface of the lips of the slit, and between the cloaca and the cloacal pit on each side. Hence the abdominal pore is on the outer side of the peritoneal wall. The abdominal cavity is continued beyond the pore for 5–6 mm., so that, on this side also, a seeker would easily pass into this cul-de-sac instead of passing through the pore.

Bridge does not mention having applied the injection method to this species, and he may therefore have failed, in probing the three specimens he examined, to pass the seeker through the pore. This, I found on trial, may often happen, even when the approximate position of the pore is known. *R. maculata* differs in the position of the pore from all the other species of Batoidei which Bridge investigated, a fact which would further tend to have misled him. *Raia maculata*, then, I believe, does not form an exception to the Batoidei on Bridge's list in wanting abdominal pores.

To this list I can add six species from my own observations.

Pristidae.—No member of this family had been shown to have open abdominal pores. I found them to be present in a male

Pristis zysron, Blkr. (about 90 cm. long). As in the other batoid fishes, the openings of the cloacal pits are placed on the ventral surface outside the cloaca. They lie on each side of and close to the hinder end of the longitudinal slit forming the cloacal opening. The mercury put into the body-cavity poured out freely from the cloacal pits.

Rhinobatidæ.—As Semper has shown the nephrostomes to be absent in *Rhinobatus granulatus*, Cuv., I took occasion to examine a female specimen, and found both abdominal pores to be open to the exterior through the cloacal pouches.

Rhynchobatus djeddensis, Forsk.—A small female (21½ inches long) had an open abdominal pore on the right side, but on the left the pore was either too small to allow the muddy spirit in the abdominal cavity to be pressed out, or it was closed. This was a museum specimen, and not available for dissection.

TORPEDINIDÆ.—*Torpedo narke*, Risso.—Semper notes the absence of nephrostomes in the adult *Torpedo maculata*. There is no *T. maculata* in the very full synonymy of the British Museum Catalogue of Fishes, but *T. unimaculata*, Risso, is given as a synonym of *T. narke*, and on this animal Semper, in all probability, made his observation. Bridge has found both male and female to possess abdominal pores. In an immature female I found them to be present.

Narcine brasiliensis, Olf.—Nephrostomes do not exist in the adult, according to Semper. A mature male in the British Museum had pores opening through cloacal pits, similar to those of other Batoidei.

RAJIDÆ.—*Raja clavata*, L.—The male only of this species was shown to have abdominal pores by Bridge. In a small female (13 inches long) the left pore was open. On the right side, in the corresponding place, the abdominal wall was exceedingly thin, but there was no perforation. There was no trace of nephrostomes remaining in the kidneys.

MYLIOBATIDÆ.—In *Myliobatis maculata*, Gray, the pores are open in the young female (10½ inches long), as they are also in the female of a species not identified belonging to this genus in the collection of the Cambridge Museum of Comparative Anatomy. As this specimen measures only 8 inches from the tip of the snout to the root of the tail, it may be the young form of

one of the known species. The hinder two-thirds of the upper surface is covered with small white spots. I could find no nephrostomes in the kidneys.

Species belonging to three of the six families of the Batoidei came under Bridge's observation. I have found abdominal pores to be present in representatives of the remaining three families, viz., Pristidæ, Rhinobatidæ, and Myliobatidæ. I have also determined the early disappearance of the nephrostomes in a species of the Myliobatidæ.

In addition to the species of Batoidei, this group of elasmobranchs (B) contains, as far as can be stated at present, six species of Carchariidæ and one of the Lamnidæ, *L. cornubica*. I have examined the following:—

Carcharias glaucus, L.—A female, 18 inches long, had papillæ placed, unlike most Selachians, outside the cloacal opening and behind it. There were no cloacal pouches; the conical papillæ arose from the skin of the ventral surface of the body, and pointed backwards. They contained peritoneal canals opening at the apex to the exterior. This must have been a newly-born individual, as a foetus in the Cambridge Museum measures $18\frac{1}{2}$ inches. Nevertheless, it agrees with Bridge's description of a male specimen, 5 feet in length, except that in this case the papillæ were $\frac{3}{4}$ inch long.

Galeus canis, Bonap.—In a full-grown female the pores were small ($\frac{1}{2}$ mm. in diameter), and opened just below the apex of each cloacal papilla, on the side turned towards the cloacal pit. The pits were shallow depressions, with the papillæ set at their anterior end. Bridge's example of this species was a male, with a large pore on the right papilla, the left one being imperforate.

Zygaena malleus, Risso.—A young male specimen, 15 inches long, had papillæ and pores resembling very closely those described above in a young *Carcharias glaucus*.

Mustelus laevis, Risso.—The cloacal papillæ were small, and perforated at the apex by minute pores, in a female measuring 20 inches. Cloacal pits could hardly be said to exist.

Mustelus vulgaris, M. & H.—A fine male specimen, over 3 feet in length, had small papillæ, with very small apical pores. No cloacal pouches were present. Another somewhat smaller specimen, a female, resembled it; and the abdominal pores were

also very minute, measuring, in the spirit-contracted condition of the tissues, less than $\frac{1}{2}$ mm. across.

Triacis semifasciata, Girard.—Abdominal pores are present in both sexes, but, like those of *M. vulgaris*, are very minute openings. A large male (34 inches long) had cloacal papillæ on the cloacal wall, placed like those of *Scy. canicula*, but without cloacal pouches; the perforation was at the apex. A small female, 14 inches long, had a right imperforate papilla, and a left papilla with a very small pore at the tip.

HOLOCEPHALA.

Semper has shown that nephrostomes are absent in *Chimæra monstrosa*. The presence of abdominal pores has been demonstrated by Bridge in this species, and they are usually ascribed to all the Holocephala. I have not been able to find any reference to them in the descriptions of the new American Chimæroid, *Harriotta raleighana*.

Chimæra monstrosa, however, agrees with the Group B of the Elasmobranchs in being without nephrostomes, and having abdominal pores.

GANOIDEI.

The observers who have investigated the structure of the renal organs in these fishes, from Semper onwards, agree in denying the presence of nephrostomes in the Wolffian body of the adult. Only in *Lepidosteus* is there a probability of the nephrostomes persisting throughout life, under somewhat peculiar conditions, to be discussed later. Jungersen has found nephrostomes in the developing Wolffian body (Urnier) of both *Amia calva* and *Acipenser sturio* at an early stage (12 and 15 mm. long): he was not able to trace their fate, but they disappear before the adult condition is reached.

Johannes Müller, Hyrtl, and Stannius all attribute abdominal pores to the Sturiones without exception, and to certain other ganoids. I have found no confusion in their works between abdominal pores and genital openings, such as Max Weber has shown to abound in old and new writings on teleosteans. They were careful to distinguish between (1) the genital ducts (Peritoneal-trichter) opening into the ureters, and through them to

the exterior by an unpaired *porus urogenitalis*; and (2) the paired abdominal pores opening on each side of the anus, and making a direct passage of communication from the body-cavity to the exterior. The ripe ova, in all ganoids excepting *Lepidosteus*, fall into the body-cavity, and pass out through the proper oviducts, not through the abdominal pores. The genital ducts of male ganoids are very imperfectly known; but observations of Rathke, Balfour and Parker, and Wiedersheim, as confirmed by Semon, show that in *Lepidosteus* at least, and probably in *Acipenser* and *Amia*, the spermatozoa are carried from the testis through vasa efferentia leading into the kidney tubules, and so through the ureters to the urogenital pore. So that in neither sex are the abdominal pores concerned with the genital functions.

Unfortunately Bridge makes use, in his account of the abdominal pores in sturgeons, of a passage from Rud. Wagner, and interprets it in the sense that in *A. huso*, *A. stellatus*, and *A. ruthenus* the abdominal pores open into the ureters.

If this were really the case, the fact would be of considerable morphological importance. But the openings into the ureters, Wagner continues, are through "two membranous infundibuliform tubes, which are united with and open into the two wide ureters about the middle of the kidneys; behind these apertures is a valve to prevent the escape of the urine into the ventral cavity"; and Wagner correctly describes these tubes acting as oviducts, adding that, in these three species, there are no abdominal pores.

As regards the absence of abdominal pores, Wagner appears to have been in error, as Johannes Müller and Hyrtl both attribute them to all Sturiones, and he is certainly mistaken in saying that the ova of *A. sturio* are "passed through the abdominal pores, the openings into the ureters being absent."

Hyrtl describes the "membranous infundibuliform tubes" as present in both sexes of *A. sturio*, and as opening into the ureters; this is, moreover, confirmed by Stannius and by A. F. J. C. Mayer's account. There is, therefore, no difference between the three species of *Acipenser* named above and *A. sturio* as far as oviducts and abdominal pores are concerned. The abdominal pores of all sturgeons open to the exterior, one on each side of the anus, and do not function as genital ducts.

Polyodon (Spatularia) folium has abdominal pores (A. Wagner and Hyrtl) and genital ducts as in Acipenseridæ (Hyrtl).

Polypterus bichir was first shown to have abdominal pores by Hyrtl. They perforate a pair of papillæ placed on either side of the anus. Joh. Müller did not detect them, and stated that they were wanting in his *Bau und Grenzen der Ganoiden*, 1846, p. 22. Hyrtl found them by the method I used for their detection in elasmobranchs, by injecting with mercury, and adds that he could not find them in any other way.

Calamoichthys calabaricus also has abdominal pores in a similar position (Bridge, *l.c.*) to those of *Polypterus*.

Amia calva.—This fish was carefully examined by Hyrtl, and at first without success, for the presence of abdominal pores. He discovered them in a large specimen as very fine canals, and was then able to see them in the first specimen, where they were so tightly closed by shrinkage and hardening of the tissues in spirit that not even mercury was allowed to escape through them. The negative results obtained by other observers in Europe may very probably be due to the same causes. I know of no observations on this point having been made on fresh material. Bridge confirms Hyrtl's observations, adding that the pores are open in both sexes. He describes their position and gives a diagram, each agreeing in substance with Hyrtl's description and drawing. This positive evidence, especially Hyrtl's circumstantial account, is to be adopted, rather than reliance placed on negative statements which may be put down as arising out of the difficulties of the case. In larvæ of *Amia calva*, 16½ mm. long, the abdominal pores have not yet appeared, but the nephrostomes are still open (Jungersen, *l.c.*).

Lepidosteus osseus. finally, like all other known Ganoids, has abdominal pores. They were described and figured by Hyrtl and mentioned by Bridge, but were first discovered by Joh. Müller. Their occurrence in this fish, which, unlike the other Ganoids, has a tubular ovary in continuity with the oviducts, is interesting in comparison with the teleostean genera *Mormyrus* and *Gymnarchus*, which also possess abdominal pores and ovaries closed to the body-cavity. The only information on the subject of nephrostomes in *Lepidosteus* is given by Balfour and W. N. Parker (*Structure and Development of Lepidosteus*, Mem. Ed.,

i. pp. 320-1). In a young fish, about 11 cm. long, they were still present, and in such a position, between the insertion of the ovary and the segmental duct, that, "from the mode of formation of the ovarian sac, the openings of the peritoneal funnels of the excretory organs ought to open into its lumen; and if these openings persist in the adult, they will no doubt be found in this situation."

It is not unlikely that this will prove to be the case, and if so the two separate divisions of the body-cavity, that enclosed by the genital fold and that remaining as the peritoneal cavity, will then have separate communications with the exterior other than the oviducts. But the general rule that nephrostomes and abdominal pores are not present side by side in the same animal would only be infringed in a morphological sense; the function of the nephrostomes would be specialised and only have reference to the cavity of the ovary, the general abdominal cavity being served by the abdominal pores alone. These remarks apply, of course, to the female *Lepidosteus* only. In males the nephrostomes, according to Balfour and Parker's account, confirmed and amplified by Semon, serve as vasa efferentia, and form a closed system of genital ducts connected with the testis on the one hand and the kidney tubules on the other; hence they are not in communication with the body-cavity. The late stages of development of the testis and its ducts will probably prove of great interest in this and also in other Ganoids, but so far nothing is known on the subject.

No special mention of abdominal pores in *Lepidosteus* is made by Balfour and Parker, but they include amongst the distinctive characters of the whole group of Ganoids—" (7) Abdominal pores always present." That this is a correct statement is not always recognised (Wiedersheim, *Grundr. d. vergl. Anat.*, 1893, p. 463), but it may now, I think, be accepted with the above observations before us. And the presence of abdominal pores in this group of fishes is correlated, as far as is known, with the absence of nephrostomes opening into the general body-cavity.

DIPNOL

The only representative of this group of which enough is known to entitle one to make a definite statement is *Protopterus annectens*, Owen. The presence of nephrostomes was suspected

in this fish by Ayers, but W. N. Parker and Wiedersheim both state most emphatically that they are absent in the adult. On the other hand, the abdominal cavity communicates with the exterior through abdominal pores, which appear to open rather late, since Parker found them closed in a young specimen of which he cut sections. Owen (*Trans. Linn. Soc.*, vol. xviii. p. 343) gives an account of the relations of the unpaired pore to the body-cavity and anal opening, the aperture of the pore being situated within the common cloacal sphincter, just in front of the anus. The position of the anus is variable: it may be either on the right side or the left, but is always accompanied by the single pore. Stannius gives a similar account in his *Anatomie der Fische* (1854, p. 184). That the single pore is equivalent to a confluent pair of pores is shown by Ayers' observation that there is in some individuals a pair opening into the cloaca, but in others, where the external opening is outside the cloaca, it is common to the two pores, the peritoneal canals uniting just inside the opening, as described by Owen. Wiedersheim's account differs from Owen's and is not quite clear, but he also regards the pores as open. His footnote saying that they may also be absent probably refers to Parker's observation referred to above.

In the other Dipnoi nothing is known of the finer anatomy or of the development of the kidneys, so that they are not available for the purposes of the present discussion. According to Hyrtl, *Lepidosiren paradoxa*, Fitz., has no peritoneal canals or abdominal pores;¹ and Bischoff, in his monograph on this fish, make no mention of such openings. *Ceratodus*, on the other hand, is well known to have pores, as first described by Günther, paired and opening behind the cloaca.

The one species of Dipnoi, then, of which our knowledge is fairly definite, *P. annectens*, is without nephrostomes, but has abdominal pores.

¹ Ehlers found no pores in his specimens, and they were also absent in a male and a female taken in the breeding condition by Mr Graham Kerr, which, through his kindness, I was able to examine. Ehlers seems to be doubtful as to the occurrence of nephrostomes in *L. paradoxa*.

TELEOSTEI.

The subject of abdominal pores in this group of fishes has been so fully and so admirably treated by Max Weber, more especially with respect to the Salmonidæ, that I need not do more than very briefly summarise his results. He has very successfully cleared up the confusion into which almost every previous writer had involved the matter, by not duly discriminating between genital pores and true abdominal pores. The latter never serve under normal circumstances as genital ducts, and the very simple oviducts in those teleosteans which allow the mature ova to fall into the abdominal cavity, *e.g.*, Muraenidæ, are not homologous with the abdominal pores of other animals. In the Salmonidæ the ovary is a simple fold of the peritoneum, and is in a more primitive condition than in the majority of bony fishes, where it forms a tube in various ways. The ova are sometimes retained within the cavity of this tube and developed there; are passed immediately into the oviduct, which is continuous with the tubular ovary, so that the ova do not become free in the abdominal cavity. This is the condition, amongst the Ganoids, of *Lepidosteus*, in which, just as in the "elasmobranchian" ganoids, abdominal pores are present. There is a particular interest attaching to the Mormyridæ amongst teleosteans, as they present a parallel condition to that of *Lepidosteus*. The females have a tubular ovary, but still retain abdominal pores. Hyrtl¹ examined eight species of *Mormyrus*, viz., *bane*, *cyprinoides*, *elongatus*, *dorsalis*, *oxyrhynchus*, *anguillaris*, *zambacensis*, and *caschive*, and the single species of *Gymnarchus* (*niloticus*), and in all of these the abdominal pores were present. These two similar cases deserve attention as an instance of evolution proceeding on parallel lines and quite independently; and if the course of evolution is rightly interpreted in this way, further support is given to the view that *Lepidosteus* is a living representative of the ganoids ancestral to the teleosteans.

Besides the Salmonidæ, there are other families of Teleosts in which the ova fall into the body-cavity before they are shed. These are the Galaxiidæ, Hyodontidæ, Bathythrissidæ, Notop-

¹ J. Hyrtl, "Anat. Mitth. ueb. *Mormyrus* and *Gymnarchus*," *Denkschr. d. k. Akad. Wiss. in Wien Math. nat. Cl.*, Bd. xii. pp. 1-22.

teridæ, and Muraenidæ. The Characinidæ were stated to resemble these by Valenciennes, but Sagemehl has shown this to be incorrect; the ovaries are closed in this family. It has not yet been shown that any member of the five families just enumerated has abdominal pores, and the last named, the Muraenidæ, are certainly without them. I draw attention to the association of closed ovaries with abdominal pores, and to the absence of pores in some of the families which have the primitive form of ovary, for the following reason: Günther has suggested that the pores "may serve for the expulsion of semen, and those ova only which, having lost their way to the abdominal opening of the oviduct, would be retained in the abdominal cavity." If this, however, were the sole function of the abdominal openings, we should not expect them to be present in fishes like *Lepidosteus* and *Mormyrus*, with a closed ovary, where the ova do not fall into the peritoneal cavity, nor in male Teleosteans, which always emit semen from the testis into proper ducts. And we might expect to find them in fishes like the Muraenidæ, where the ova fall into the body-cavity, but there they are absent.

Two families of Teleostei, then, have species with true abdominal pores, Mormyridæ and Salmonidæ. The Mormyridæ examined for this feature have them without exception. The Salmonidæ, according to Max Weber's careful investigations, do not all possess pores. They are lacking in both sexes of *Osmerus eperlanus*, L., and in *Mallotus villosus*, Cuv. Of *Salmo fontinalis* and *S. quinnat* immature specimens only were available, and only one of the former had a pore on the right side, none on the left; of the latter, the single unripe female had no pores. Three male *Salmo fario*, L., included one immature specimen (45 cm. long) without pores, but another (44 cm. long) had both open, and a third mature individual had one (right) open and the other closed; indeed, the presence of a definite open pore does not seem to be essential in *S. fario*, judging from the experiments of Guido Schneider. The absence of pores in immature *Salmo* is, I suspect, to be put down to their late appearance; for in the case of *S. salar*, of which a greater number were examined, pores were always present in the larger specimens; when they were quite absent, or present on one side only, the individual was always one of the smaller specimens. Twelve female *S. salar* were found

to have pores, with one exception, in which the perforation was not complete. Three males of this species included one without pores (106 cm. long); and a fourth young male, only 22 cm. long, had no pores. The species in which pores always occurred in both sexes are: *Argentina silus*, Risberg, *A. hebridica* (Yar. spec.), and *Coregonus lavaretus*, L. (sensu Collett). Males only of *Salmo trutta*, L., were seen; all had pores. The case of *Coregonus oxyrhynchus* is more complicated. All males had open abdominal pores. But out of seventeen females, a certain number were without them. Nine unripe females included only one without pores; but of eight mature females, only one had both pores and two more had the left pore only, the remaining five had the pores closed. This, Weber considers, is due to the pores closing up, perhaps by a kind of inflammatory process, when the ovaries become ripe.

The Salmonidæ generally seem, to judge from the above facts, to be in an intermediate condition; and as the presence of abdominal pores is more characteristic of lower types of fishes, while the more specialised Teleosteans do not possess them, I have not much hesitation in saying that the Salmonidæ are on the way to lose the pores altogether. Some of the species do not acquire them until they are quite mature and large: *C. oxyrhynchus* appears to close them when mature, and they are not always present in unripe females, so that they may only open for a short time during the ripening of the ovary. Lastly, they are quite absent in at least two species, *Osm. eperlanus* and *M. villosus*, which, on this view, would approach the higher bony fishes.

Nephrostomes are not known to remain open in this group of fishes, if the pronephros of Fierasfer be, for the present, disregarded. The peritoneal cavity is therefore only put into communication with the exterior through abdominal pores in certain Salmonidæ and Mormyridæ, through the oviducts in the females of the Muraenidæ and of a few other fishes with open ovaries. In the great majority of the Teleosteans, however, we find that the general peritoneal cavity is completely closed in, both in the male and the female: only that portion represented by the lumen of the ovary is open to the exterior through the oviduct.

FIG. 4.—Diagram showing the communication between body-cavity and exterior through nephrostomes only in *Cestracion*, *Echina*, and certain other Selachians before attaining full size or maturity respectively, also in *Amia calva* larvæ.

FIG. 5.—Diagram showing the communication both through nephrostomes and abdominal pores between body-cavity and exterior in certain adult Scylliidae and Spinacidae.

PORE CANAL

FIG. 6.—Diagram showing the communication through abdominal pores only between body-cavity and exterior in Carchariidæ, Lamnidæ, and Batoidei; in Holocephala, adult Ganoidei, certain Dipnoi, certain Salmonidæ and in Mormyridæ.

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ON THE ORIGIN OF VERTEBRATES, DEDUCED FROM
THE STUDY OF AMMOCETES. By WALTER H.
GASKELL, M.D., LL.D., F.R.S., *University Lecturer on Physi-
ology; Fellow of Trinity Hall, Cambridge.*

PART I.—THE ORIGIN OF THE BRAIN.

PART II.—THE ORIGIN OF THE VERTEBRATE CRANIO-FACIAL
SKELETON.

INTRODUCTION.

IN the course of investigations upon the sympathetic nervous system,¹ I was led to consider the relationship between the segmented cranial and spinal nerves, and in consequence to put forward evidence to show that the cranial nerves were built up of the same constituent parts as the spinal, and that the plan of the original segmental type might be referred back to the innervation of two sets of organs, segmentally arranged, forming thus a double segmentation, called by me splanchnic and somatic, by Ahlborn branchiomic and mesomic, rather than to an original type formed, as in the spinal nerves, of afferent and efferent roots. The following out of this idea led to the recognition that this dual segmentation in the cranial region was not only a peripheral segmentation connected with the innervation of the somatic and splanchnic muscles, but was deep seated in the structure of the central nervous system itself; in that the centres for the segmentally arranged visceral muscles, *i.e.*, muscles belonging to the splanchnic segmentation, and derived, according to v. Wijhe's observations, from the lateral plates of mesoblast, viz., the motor nuclei of origin of the Vth, VIIth, IXth, Xth, and XIth nerves, formed a separate, segmentally arranged series of cell-groups, all belonging to the same system, and distinct from the cell-groups which gave origin to the nerves innervating the somatic muscles, *i.e.*, the muscles derived from the mesoblastic somites.

¹ *Journ. Physiol.*, vol. vii. p. 1, 1886, "On the Structure, Distribution, and Function of the Nerves which innervate the Visceral and Vascular Systems."

The further consideration¹ of the comparison between spinal and cranial nerves and their centres of origin in the central nervous system, led me to the same conclusion as the older anatomists, viz., that the central nervous system of the vertebrate was built up of a paired series of centres or ganglia, each pair of which gave origin to a pair of segmental nerves; and I, like my predecessors, was immediately struck with the close resemblance of the arrangement of the vertebrate nerve centres, and their connections with those of the great appendiculate group of invertebrates. This line of thought led to further consideration of the reasons why such a manifest resemblance, functionally, structurally and topographically, between the invertebrate and vertebrate nervous systems, had been in the present day discredited and allowed to fall into the background; and it immediately became clear that the main reason, the one stumbling-block, was the tubular formation of the vertebrate central nervous system. The question thereupon arose in my mind, Is this tube really a part of the nervous system; or can we look upon the tube-formation as one thing, and the segmental grouping of nerves and ganglia as another and separate? Imagine a central nervous system of the invertebrate type grouped around a non-nervous epithelial tube, what would that mean? Immediately it was plain that this epithelial tube behaved itself topographically to the vertebrate central nervous system precisely as the alimentary canal tube of the Appendiculata to its central nervous system; and I was therefore led to the conclusion that it was well worth seeing how the resemblances would accord with the hypothesis that the vertebrate central nervous system was derived from one of an appendiculate type by the simple process of growth of nervous material over the pre-existing alimentary canal. Following out this thought, I saw at once that the cerebral hemispheres, with the optic and olfactory nerves, corresponded exactly with the supra-oesophageal ganglia, with their optic and olfactory nerves; that the crura cerebri, with the infundibular epithelial tube passing between them to reach the ventral surface of the brain, corresponded exactly with the oesophageal commissures; and

¹ *Journ. Physiol.*, vol. x. p. 153, 1889, "On the relation between the Structure, Function, Distribution, and Origin of the Cranial Nerves, together with a Theory of the Origin of the Central Nervous System of Vertebrata."

what seemed to me almost positive proof, the pineal eyes fitted harmoniously into their natural place as the relics of the median eyes of the invertebrate ancestor. The consideration of the pineal eye led me to the conclusion that that invertebrate ancestor belonged to the Arthropoda rather than to the Annelida; and this consideration, along with others, led me, from the very first, to the conclusion that investigation into further resemblances ought to be carried on in the *Limulus* type of arthropod. I arrived at these conclusions in 1887; and in the autumn of that year I sent a MS. embodying my views to Prof. Huxley, who wrote back urging me to delay publication until I had considered the matter further. I did not, therefore, publish that autumn, but waited until the next year, when I read a paper¹ on 23rd June 1888 to the Anatomical Society, stating the conclusion I had arrived at. The next year, 1889, a fuller consideration of these views was published in the *Journal of Physiology* and in *Brain*,² and in the latter I especially pointed out that the study of the pineal eye in the *Ammocoetes* or larval lamprey had convinced me that this eye arose from a median eye of the arthropod type. Between 1888 and 1890 I had been studying the structure and arrangement of the central nervous system of the *Ammocoetes*, in the full conviction that, if I was right, the separation of the epithelial tube from the nervous material proper must be much more conspicuous here than in the higher Vertebrata, and the whole nervous system proper must be much more comparable with that of an Arthropod, such as *Limulus*. Such I found to be the case, far beyond my expectations; and the examination of the *Ammocoetes* brought to light, further, so many hitherto unsuspected links between the vertebrate and arthropod, that I determined to publish a series of papers on the different tissues and organs of *Ammocoetes*, with the express intention of showing how they were derivable from corresponding arthropod tissues and organs: accordingly, in 1890,³ I published chapter 1 on the central nervous system of *Ammocoetes* in the *Quarterly*

¹ *Journ. of Anat. and Physiol.*, vol. xxiii., 1888.

² *Brain*, vol. xii., July 1889, p. 1, "On the Origin of the Central Nervous System of Vertebrates."

³ *Quart. Journ. Micros. Sci.*, 1890, "On the Origin of Vertebrates from a Crustacean-like ancestor."

Journal of Microscopical Science. In this paper I showed how the conclusions at which I had arrived in 1887 were confirmed by the study of so low a vertebrate as *Ammocætea*. In the same number of the *Journal* in 1890, Patten¹ published a paper giving the reasons why he considered vertebrates to be derived from arachnids, without, however, giving any reference to my previous publications.

Owing to a difference of opinion between the editors of the *Quarterly Journal* and myself upon the value of my further contributions on this subject, I determined to seek another channel of publication; and in order to put my views before the scientific world without further delay, I took the opportunity afforded me, as President of the Physiological Section of the British Association, at its meeting in Liverpool 1896, with the full consent, and indeed, I may say, at the instigation of the sectional organising committee, to lay before the public a statement of the conclusions at which I had arrived upon the origin of vertebrates. Such a statement in such an address is necessarily somewhat dogmatic, and cannot possibly deal with the details upon which the conclusions are based. I propose, therefore, in this and in the following papers, to take as the text of my discourse that address at Liverpool,² and to fill in as I go along the details of evidence which were there wanting.

In the first place, I will briefly sketch the history of the views which have been held upon the origin of Vertebrates; as I consider that, in a matter of this sort, we obtain a much better judgment of the present position of the question if we see how it has arisen, than if we consider it without any historical retrospect.

HISTORICAL.

In considering the history of the various views held from time to time upon the origin of Vertebrates, we may commence with Geoffroy St Hilaire,³ who, in 1822, advocated the view that a general plan of organisation existed in the animal kingdom, and considered that the vertebrates fitted into that plan if only they were considered as

¹ *Quart. Journ. Micros. Sci.*, 1890, "On the Origin of Vertebrates from Arachnids."

² *Report of the British Assoc.*, 1896, p. 942, and *Nature*.

³ "Philosophie Anatomique" and "Sur la Vertèbre" in *La Revue Encyclopédique*, 1822.

invertebrates in which the dorsal and ventral surfaces had been interchanged, so that the relation of alimentary canal, nervous system, and heart in this way became the same for the Annelida, Mollusca, Arthropoda, and Vertebrata. This view was strongly opposed by Cuvier,¹ but received support in many directions, especially from the work of Newport,² Treviranus, and, later, of Leydig,³ in which it was shown how easily the different parts of an arthropod brain homologised with the corresponding parts of the vertebrate brain.

Up to 1866 the relationship of the higher invertebrates to vertebrates, based upon anatomical and physiological considerations, was considered certain. In that year there appeared the memoir by Kowalewsky⁴ upon the larval forms of ascidians, in which he concluded that such forms were vertebrate in character, and that therefore the Vertebrata had arisen from the tunicates. This paper led to considerable discussion, its conclusions being objected to strongly by v. Baer,⁵ while it was confirmed and its conclusions strengthened by Kupffer.⁶ Gegenbaur was inclined to accept it in his *Comparative Anatomy*, 2nd ed., 1870, p. 723, for he considered that it was impossible to homologise the vertebrate brain and spinal cord with both supra- and infra-oesophageal ganglia and ventral chain of the annelid or arthropod invertebrate groups, but only with the supra-oesophageal.

In 1875 this view, that the vertebrates were derived from tunicates, which had become at that time the popular one, was destined to receive a rude shock from the simultaneous work of Semper,⁷ Balfour,⁸ and Dohrn.⁹ Back swung the pendulum, and again the segmented annelids became first favourite in the race. This change in opinion was brought about through the simultaneous observations of Semper and Balfour upon the close resemblance between the structure of the segmental organs of worms and of vertebrates, and through Dohrn's paper, which pointed out that the evidence was stronger to show that *Amphioxus* and tunicates were degenerate forms of vertebrate ancestors, whose nearest vertebrate type was to be found in *Ammocoetes*, than that they were like the ancestral vertebrate forms. Dohrn therefore became a strong advocate of the original view of Geoffroy St Hilaire—that the vertebrates were derived from appendiculate forms, in which a reversal of back and front had taken place. Dohrn further, recognising the necessity in such a comparison of accounting

¹ *La Revue Encyclopédique*, Tome xvii., 1823, and *Annal. d. Sci. Nat.*, Tome xix. p. 241, 1830.

² *Phil. Trans.*, 1843.

³ *Bau des thierischen Körpers*, Tübingen, 1864.

⁴ *Mem. Acad. Imp. d. St Petersburg*, x., 1866.

⁵ *Mem. Acad. Imp. d. St Petersburg*, xix., 1873.

⁶ *Archiv. f. Micros. Anat.*, Bd. vi.

⁷ *Arbeiten aus d. zool.-zootom. Institut, in Würzburg*, 1874.

⁸ *Quart. Journ. of Micros. Sci.*, 1874, and *Journ. of Anat. and Physiol.*, vol. x., 1875.

⁹ *Der Ursprung der Wirbelthiere und das Princip des Functionswechsels*, Leipzig, 1875.

for a supra- and infra-oesophageal mass, supposed that the vertebrate mouth was a new formation, formed out of a coalesced pair of gill slits, while the original invertebrate mouth and oesophagus must have disappeared; the position of the tube from mouth to gut between the oesophageal commissures being shown by the thin dorsal wall of the fourth ventricle and the region of the hypophysis.

In addition to this attempt of Dohrn to account for the remains of the old invertebrate oesophageal tract in the vertebrate brain, as early as 1866 Owen had argued on similar lines, and in 1881 and 1883 gave in his adherence to the annelid view, and considered that the position of the old oesophagus was indicated by the conario-hypophysial tract,¹ a view which had already been suggested by Geoffroy St Hilaire,—the position of the old mouth being the region of the pineal body. Balfour, in discussing the ancestry of vertebrates, although inclined to the annelid theory, yet was unable to accept either Dohrn's view or Owen's view, and did not consider that there was any evidence in the vertebrate nervous system of any piercing through on the dorsal side of a mouth tube, and indeed that the whole theory of reversal of surfaces was too improbable. He therefore, in 1878, suggested that the nemertines might represent a type from which both annelids and vertebrates have sprung as two diverging branches, the two lateral nerves of the nemertine ancestors being supposed to approach each other and meet on the ventral surface to form the halves of the annelid nerve cord; and on the opposite or dorsal surface, to form the central nervous system, the brain and spinal cord of the vertebrates.

Hubrecht,² in 1880, accepted Balfour's view of the origin of vertebrates from the nemertines, but suggested that the lateral nerves corresponded to the lateral line nerves of fishes, and that the vertebrate nervous system arose from a median dorsal nerve which is found in some nemertines in addition to the two lateral nerves.

This suggestion of Hubrecht and Balfour marks a turning point in the history of the question; for whereas up to this point the supposed ancestor belonged to a large group of existing animals, viz., the Appendiculata or Tunicata, the details of whose organisation could be compared with those of Vertebrata, no such group of segmented worms, as their hypothesis demanded, had ever been found; so that, instead of there being a possibility of checking the validity of their theory by direct anatomical comparison of the details of structure between vertebrates and their immediate supposed ancestral invertebrate group, the only possible attempt to prove it must be based, as far as anatomy is concerned, on the structural resemblances between vertebrates and confessedly remote ancestors, and the main burden was, of necessity, transferred from anatomy to embryology; for, as there were no living immediate ancestors, the only chance was the interpretation of the early developmental history of the vertebrate on

¹ *Essays on the Conario-Hypophysial Tract, and the Aspects of the Body in Vertebrate and Invertebrate Animals*, London, 1883.

² *Quart. Journ. of Micros. Sci.*, 1880.

the hypothesis that ontogeny reproduced phylogeny. The tendency of this line of thought was naturally to put in the background resemblances obtained from the comparative anatomy of the adult, and to magnify the importance of speculations derived from the interpretation of early developmental phenomena, so that free scope was given to the reins of fancy, and speculations were freely indulged in as to the manner in which vertebrates might have been evolved out of various primitive invertebrate groups. Such speculation has led largely to a confession of hopelessness with regard to the question. The view that vertebrates are derived from flat worms, or from coelenterates, is a derivation from ancestors so remote as to have really very little bearing upon the nature of the form from which vertebrates have immediately arisen. Among these various speculative theories, one only has come forward prominently, that of Bateson,¹ upon the affinity of *Balanoglossus* to *Amphioxus*, and so to vertebrates. This speculation, which has been opposed by Spengel² in Germany, on the grounds that neither the so-called notochord of *Balanoglossus*, nor the central nervous system, nor the gill slits, are homologous with those of vertebrates, and has received its main support in England, brings back *Amphioxus* and the tunicates more directly into the ancestral line, and, through the supposed affinities of the larval *Balanoglossus* with Echinodermata, links on a primitive large invertebrate group with the vertebrates. The difficulty of the speculation lies in the fact that between Echinodermata and the lowest vertebrate—a gap which cannot be bridged over without an enormous number of forms—no intermediate forms have been found, or even suggested, except such doubtful isolated forms as *Cephalodiscus*, *Rhabdopleura*, and *Balanoglossus*.

In this sketch of the history of the question one fact stands out prominently. Whatever other theories have been put forward to explain the origin of vertebrata, no one of them has been able to overcome the strong feeling that a relationship must exist between the Vertebrata and the Appendiculata, owing to the fact that the latter group alone possesses a central nervous system comparable to that of vertebrates. Throughout the whole history, champions of the origin from the Appendiculata have always come forward; and the one reason why they have not been able to make any real advance in their views has been the difficulty of accounting for the altered relations of alimentary canal and nervous system in the two groups. My theory solves this difficulty; for, by the recognition that the central canal of the vertebrate central nervous system is the old alimentary canal of the

¹ *Quart. Journ. of Micros. Sci.*, vol. xxvi., 1886.

² *Die Enteropneusten*, Berlin, 1893. See also Lang, *Text-Book of Comparative Anatomy*, translated by H. M. and M. Bernard, pt. ii., 1896, p. 591.

appendiculate animal, the necessity of reversal of surfaces is done away with; the infundibular canal, which has throughout the whole history been looked upon as the remnant of the original œsophagus, is seen rightly to form a part of the old œsophageal tube; and finally, the invertebrate median eyes, which become the pineal gland, receive their appropriate and necessary explanation as the median eyes of the arthropod ancestor. All the old difficulties associated with the view of an appendiculate ancestor vanish; and an enormous number of new topographical and histological coincidences are immediately made manifest,—coincidences which, although somewhat apparent before, were rendered exceedingly difficult, if not impossible, of explanation as long as the back of the one animal was looked upon as the front of the other. One new difficulty is introduced, viz., the formation of a new alimentary canal in the vertebrate group; and I imagine that the question of the acceptance of this theory of mine depends upon whether the difficulty of accepting the possibility of the formation of a new alimentary canal is sufficiently great to overpower all evidence of the topographical and histological coincidences. In these papers I propose to put forward the evidence which, in my opinion, gives a clue as to the manner in which that new canal was formed, and I shall take in order the origin of the cartilaginous skeleton, of the striated muscles, the cranial nerves, and the other organs of the body; and finally, after such evidence has been given, see what conclusion is arrived at as to the formation of the new alimentary canal.

In any attempt to decide the line of descent of any group of animals, certain principles can be laid down which must agree with the argument. The following principles were laid down by Shipley in the discussion at Cambridge upon my paper read at the Philosophical Society on 25th November 1895:¹—

1. In assuming variations to arise in an ancestor, the amount of change assumed, and its direction, must agree with the kind of variation known to exist in the various members of the group to which the ancestor belongs, and the amount of variation assumed should be limited.

To this principle I would add—

2. The kind of variation by which members of the higher

¹ *Proc. Cambridge Philos. Society*, vol. ix. p. 19, 1895.

group have steadily risen from the lowest to the highest form must be in accordance with the supposed variations by means of which the lower group has approximated to the higher.

3. Changes of function can arise when the new function coexists, perhaps subordinately, with the primary function; or coexists in another member of the same group, or in one of its larval forms.

Here I would add another principle, not mentioned in Shipley's list:

4. Organs that are clearly rudimentary in the higher group must be derived from corresponding organs which are functional in the lower.

5. In phylogeny we must look at the most elementary of the animals whose ancestors we seek.

6. In any attempt at phylogeny, the embryological unities must be observed.

Such a statement of the principles upon which an investigation of the origin of vertebrates must take place is most just; and the only fault that can be found with these six principles is the difficulty, in the case of the last principle, of being sure of what is meant by the 'embryological unities.' I would rather substitute—

6. Any explanation of the origin of a higher group from a lower group must be confirmed by the study of the development in the higher group.

In that discussion it was asserted that my theory ran counter to these fundamental principles. As, in my opinion, these principles are right, it is absolutely necessary to consider for every part of my theory whether it is in harmony with these principles or not. In the first instance, then, I will take my theory of the origin of the vertebrate brain, and see whether or no it is in harmony with these six principles.

PART I.—ON THE ORIGIN OF THE BRAIN.

PRINCIPLE 1.—In assuming variations to arise in an ancestor, the amount of change assumed, and its direction, must agree with the kind of variation known to exist in the various members of the group to which the ancestor

belongs, and the amount of variation assumed should be limited.

How does this principle apply to my hypothesis of the manner in which the brain of vertebrates has been formed? My hypothesis asserts that the vertebrate brain has been formed by the concentration and steady growth of the supra- and infra-oesophageal ganglia, together with their connecting oesophageal commissures around the oesophagus and original cephalic stomach, to such an extent that the oesophagus has become functionless, and the walls of the cephalic stomach have become in part the lining epithelium of the ventricular cavities and partly their membranous roofs, or choroid plexuses. We ought therefore to find, in the first place, that in the arthropod group there is evidence of such progressive concentration or cephalisation of the infra-oesophageal ganglia as to form, together with the supra-oesophageal ganglia and the oesophageal commissures, a brain mass directly comparable with the brain mass of a low vertebrate like *Ammocetes*. We ought to find, in the second place, that such progressive cephalisation has interfered very seriously with, or at all events has been accompanied by, a diminution in the calibre of the oesophagus of so marked a character as to point directly towards a complete closure; and in close connection with this we ought to find, in the third place, that in this very group the alimentary canal and the nervous system give indications of their future fusion.

1. *The Principle of Cephalisation.*

It is impossible to conceive a more perfect example of the truth of this principle than is afforded by the Appendiculata. The segmented annelid type of nervous system consists of a supra-oesophageal ganglion, composed of the fused ganglia belonging to the pre-oral segments, and an infra-oesophageal chain of separate ganglia. With the modification and concentration around the mouth of the most anterior locomotor appendages to form organs for prehension and mastication of food, a corresponding concentration and fusion of the ganglia belonging to these segments takes place, so that finally, in the higher annelids, and in most of the great arthropod group, a fusion of a number

of the most anterior ganglia has taken place to form the infra-oesophageal ganglion mass. Further, the nervous system of most of the Arthropoda may be divided into the following groups:— (1) Pre-oral or supra-oesophageal; (2) infra-oral or infra-oesophageal; which again may be divided into prosomatic, mesosomatic, and metasomatic, if we use these terms in their most general signification.

The infra-oesophageal ganglion mass, then, in most of the Arthropoda may be spoken of as formed by the fusion of the prosomatic or mouth ganglia, the mesosomatic and metasomatic remaining separate and distinct. The number of ganglia which have fused is seen by examination of the embryo, in which it is easy to see indications of the individual ganglia or neuromeres, although all such indication has disappeared in the adult: thus the infra-oesophageal ganglia of the crayfish has been shown to be constituted of six prosomatic ganglia.

In fig. 1 I give figures of the central nervous system (with the exception of the abdominal or metasomatic ganglia) of Branchipus, Astacus, Limulus, Scorpio, Androctonus, Thelyphonus, and Ammocetes. In all the figures the supra-oesophageal ganglia are lined horizontally, and their nerves shown, viz., optic (lateral eyes (II) and median eyes (II)), olfactory (I) (1st antennæ, camerostome nose); then come the prosomatic ganglia, dotted, with their nerves (A) supplying the mouth parts, and the 2nd antennæ or chelicerae; then come the mesosomatic, lined horizontally, with their nerves (B) supplying respiratory appendages. These figures show that the concentrated brain mass around the oesophagus of an arthropod, which had arrived at the stage of Astacus, is represented by the supra-oesophageal ganglia and the fused prosomatic ganglia.

The next stage in the evolution of the brain is seen in the gradual inclusion of the mesosomatic ganglia, one after the other, into the infra-oesophageal mass of the already fused prosomatic ganglia. With this fusion is associated the loss of locomotion in these mesosomatic appendages and their entire subservience to the function of respiration. Whether, as Dana¹ urges, cephalisation is a consequence of loss of locomotion, and the alteration of the functions of the appendages to those of mastication and

¹ "On Cephalisation," *Mag. of Nat. Hist.*, 1863, p. 187.

respiration, or not, the fact remains that in *Limulus*, where the

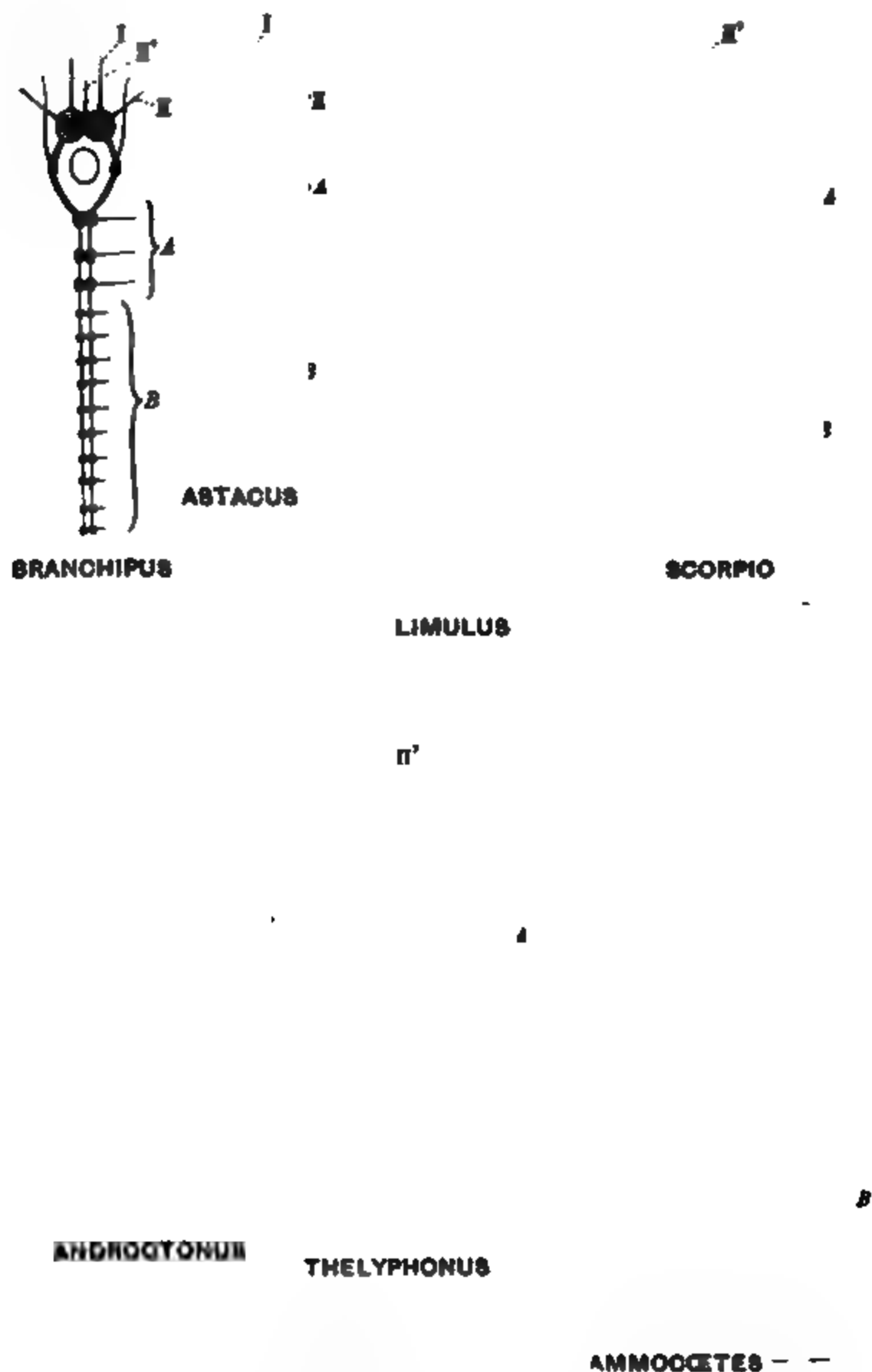


FIG. 1.—Comparison of Invertebrate brain from Branchipus to Ammocetes.

ages form a series of free appendages, of which the first is the operculum and carries the terminal ducts of the genital organs, and the remaining five are mainly respiratory, though free to move, the ganglion supplying the first mesosomatic appendage has, as is seen in the fig., fused with the prosomatic infra-oesophageal mass. In the next stage, that of the scorpion, in which the mesosomatic appendages have lost all power of free locomotion and have become internal branchiæ, yet another mesosomatic ganglion has fused with the brain mass, while in *Androctonus* two of the branchial mesosomatic ganglia have fused;¹ and finally, in *Thelyphonus* and *Phrynus* all the mesosomatic ganglia have coalesced with the fused prosomatic, while the metasomatic ganglia have fused themselves in the caudal region. The brain in these animals may be spoken of as composed of three parts—(1) the fused supra-oesophageal ganglia, (2) the fused prosomatic ganglia, and (3) the fused mesosomatic ganglia. Such a brain is strictly homologous with the vertebrate brain, which also is built of three parts—the prechordal brain or the cerebral hemispheres together with the basal and optic ganglia; corresponding to the supra-oesophageal mass, with its olfactory and optic divisions lying in front of the infundibular canal, or old oesophagus; the epichordal brain, which is again divisible into a trigeminal and a vagus division, of which the first strictly corresponds to the fused prosomatic group, and the second to the fused mesosomatic group. Further, just as in the embryo arthropod, it is possible, with more or less accuracy, to see the number of neuromeres or original ganglia which have fused to form the supra- and infra-oesophageal portions of their brain, so also in the embryo vertebrate we are able (see Locy²) at an early stage to gain an indication, more or less accurate, of the number of neuromeres which have built up the vertebrate brain. The further consideration of these neuromeres, and the evidence they afford of the number of the prosomatic and mesosomatic ganglia which have formed the epichordal part of the vertebrate brain, must be left to the chapter on the segmentation of the cranial nerves. This same process of cephalisation does not cease with the

¹ Lankester, *Trans. of Zool. Soc.*, vol. xi.

² *Jour. of Morphology*, vol. xi., 1895, "Contributions to the Structure and Development of the Vertebrate Head."

formation of the medulla oblongata out of the fused mesosomatic ganglia, but still continues into the vertebrate group themselves with the same steady progress as in the Arachnida; and we see the inclusion into the brain region of more and more separate segments in the formation of the occipital region and the centres of the spino-occipital nerves.

2. *The Antagonism between Cephalisation and Alimentation.*

The principle of cephalisation, when carried to its extreme, must produce a brain like that of Thelyphonus and the spiders, as shown in fig. 1. If, simultaneously with this fusion of the separate ganglia, the nervous material itself has increased in extent, as appears to be the case upon comparison of the scorpion brain with that of Limulus, then so large a mass of growing nervous material must entirely surround the œsophagus as to render it likely that the size of its calibre should be seriously interfered with, just as the growth of an œsophageal tumour causes stricture of the œsophagus. Still more is it likely that such increase of brain material would compress the œsophagus if, as is the case in Thelyphonus and the scorpions, the head region was cased in with an unyielding chitinous carapace.

The predominant idea in the evolution of the invertebrate has been the growth of a nervous system composed of pre-oral and post-oral parts joined together, so as to form a ring of nervous material around the œsophagus; if, further, as I believe must be the case, the keynote of the upward progress in the animal kingdom is the increase of brain power, it follows of necessity that this plan of piercing the anterior end of the central nervous system with the œsophagus must lead ultimately to a deadlock, owing to the increasing antagonism between brain-growth and alimentation. That such a limit has already been reached in the upward progress of the invertebrate is seen in the formation of the spider and scorpion group. Here, where the concentration and growth of the brain mass is greater than in any other arthropod group, we see that such growth and concentration have resulted in, or at all events been accompanied by, such a change in the habits of the animal, that no longer, owing to the minute size of the œsophagus, is it possible for the members of

the group to feed on solid food, but by means of suctorial apparatus they are obliged to keep themselves alive by sucking out the juices of other animals.

The diagrams on fig. 1 indicate the small size of the œsophagus in the most concentrated brains. Truly the direction and progress of variation in the Arthropoda was leading, owing to the manner in which the brain was pierced by the œsophagus, to a terrible dilemma,—either capacity for taking in food without sufficient intelligence to capture it, or intelligence sufficient to capture and no power to consume. Such a dilemma led, in the



B

FIG. 2.—Transverse section through the brain of a young *Thelyphonus*. *A*, supra-œsophageal ganglia; *B*, infra-œsophageal ganglia; *Al*, œsophagus.

most natural and simple way, to the formation of the vertebrate, in which intelligence gained the day, the old œsophagus was closed, its vestiges still remaining as the infundibular canal, and the brain could increase without interfering with alimentation, for a new method of obtaining and assimilating food was gradually evolved, as will be more fully set forth in this and subsequent papers.

The size of the œsophagus in comparison to the brain mass is seen in fig. 2, which represents a transverse section through the brain of a young *Thelyphonus*. This figure shows not only how this part of the alimentary canal has become a mere

central canal in the midst of the brain mass, but also how it is surrounded so closely by nervous matter that its epithelium may be looked upon as the lining epithelium of the nervous mass. Another instance in the same group of the Arthropoda of the close connection between part of the central nervous system and the gut is given in a series of sections which Hardy made through the brain region of Branchipus, in the course of the investigations which he published in the *Phil. Trans.*¹ His sections, to which he has kindly allowed me to refer, show the exceedingly close connection between the nerve cells of the optic ganglion and the lining epithelium of the anterior diverticulum of the gut on each side. The cells of the gut wall are here so closely attached to the cells of the optic ganglion that no line of demarcation is visible between the two structures. The wall of the narrow gut diverticulum forms here, in fact, a lining epithelium to a part of the optic region of the brain,—a very significant fact in connection with the prevalence of two long anterior diverticula in the early arachnids, and the formation of the optic nerves in Vertebrata. This point will, however, be dealt with when I come to deal with the origin of the visual apparatus in vertebrates: it is sufficient here to point out that the amalgamation of brain matter and gut has already shown signs of commencement among the group of Arthropoda.

PRINCIPLE 2.—The kind of variation by which members of the higher group have steadily risen from the lowest to the highest forms must be in accordance with the supposed variations by means of which the lower group has approximated to the higher.

My theory is in complete harmony with this principle, and indeed explains the variations which have taken place as we pass upwards from the brain of Ammocetes to the brain of man in a thorough and complete manner, such as is not even imagined by any other theory. Always we find a continuation of the same process, viz., a growth in extent and complexity of nervous material on the outside of the epithelial tube, which formed

¹ Hardy, *Phil. Trans.*, 1894, B. p. 83, "On the Histological Features and Physiological Properties of the Post-oesophageal Nerve Cord of the Crustacea."

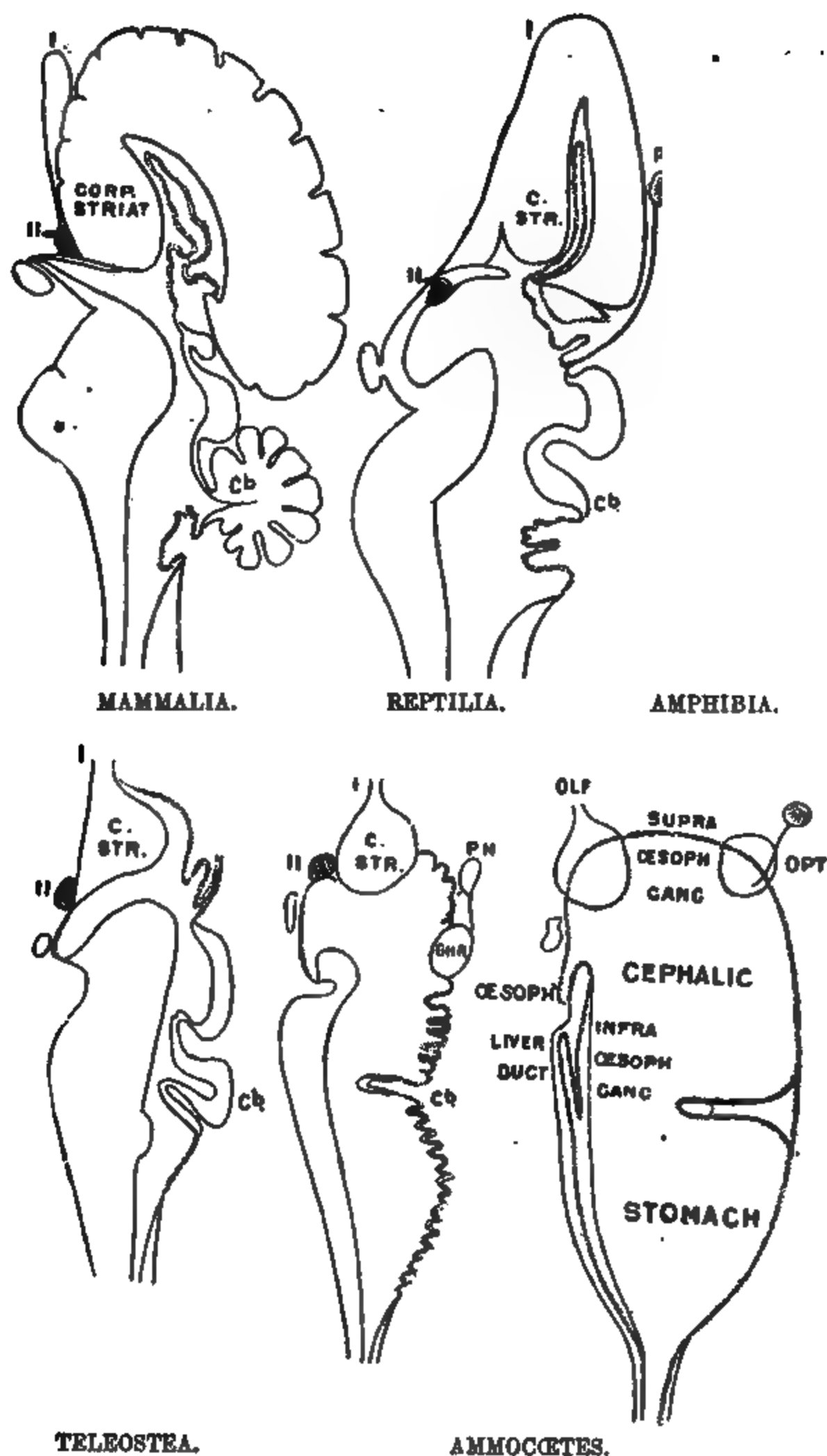


FIG. 3.—Comparison of Vertebrate brain from Mammalia to Ammocetes (Epithelial parts represented by dotted lines).

originally the cephalic stomach. The sections in fig. 3, taken mainly from Edinger, show diagrammatically the growth of the nervous material as we pass from *Ammocoetes* to the mammal.

The first stage in the process is seen when the *Ammocoetes* is transformed into *Petromyzon*; for if we compare the brain of *Ammocoetes* (fig. 4), the whole dorsal roof of which, in the epichordal region, consists of fold upon fold of simple epithelial

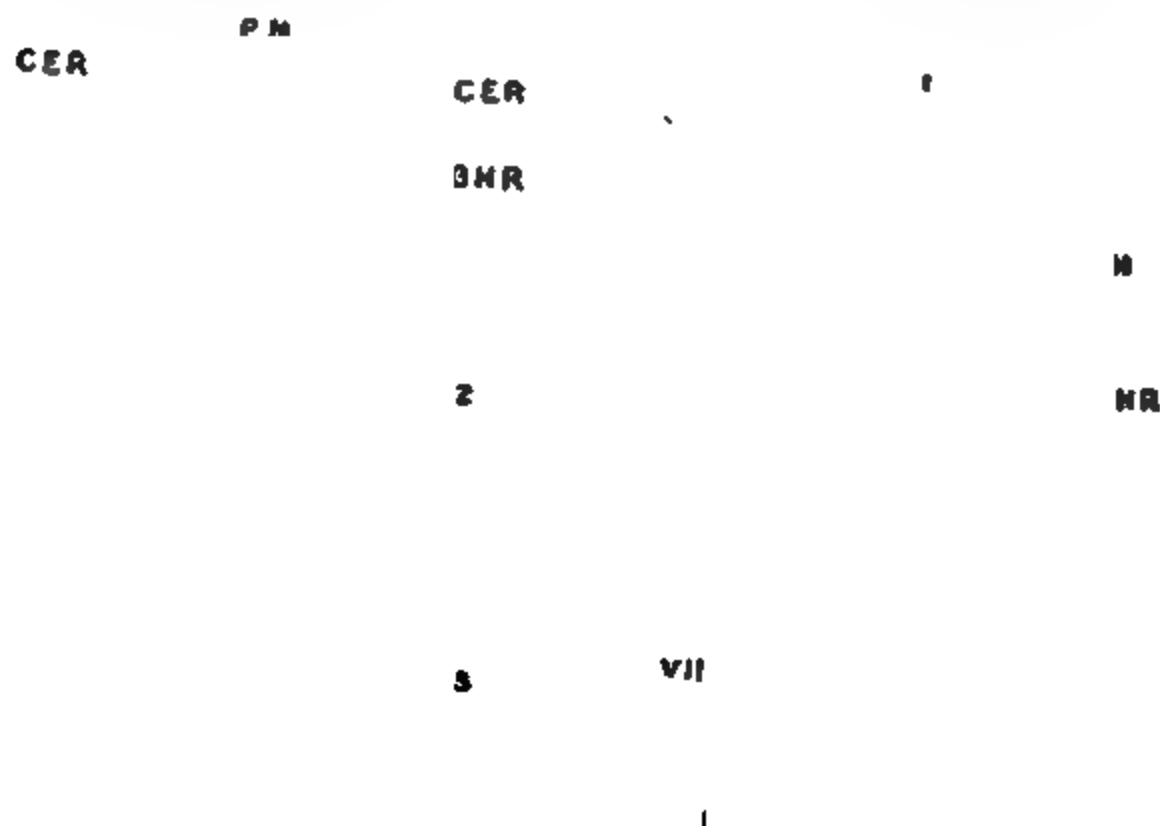


FIG. 4.—Dorsal and lateral view of the brain of *Ammocoetes*. CER, cerebral hemispheres; GHR, right ganglion habenula; PN, right pineal eye; CH₂, CH₃, choroid plexuses; I-XII, cranial nerves.

membrane, except in one place where it is constricted by the passage of the fourth nerve and commencing cerebellum, with that of *Petromyzon*, we see how, by the growth over a portion of the membranous roof of nervous material from the ventral to the dorsal side of the anterior part of the epichordal portion of the brain, the posterior corpora quadrigemina have been formed, and thus the aqueduct of Sylvius arises.

Very instructive is the rise and growth of the cerebellum.

We see how, from the prosomatic region, the region of co-ordination and equilibration, a small mass of nervous material creeps dorsalwards over the membranous roof alongside the fourth nerve, and thus in *Ammocoetes* forms the commencement of the cerebellum, and possibly also of the posterior corpora quadrigemina. We see how in the *Amphibia* the cerebellar dorsal strip is slightly larger, but here the main development has taken place in the corpora quadrigemina rather than in the cerebellum. We see, however, in the fishes that the dorsal growth of the cerebellum has increased considerably, and has surrounded, after the fashion of a hernia, a bag of the membranous roof, and so formed the worm of the cerebellum; we see further in the elasmobranchs the commencement of the cerebellar hemispheres, for on each side of the median worm a bag of membrane continuous with that of the roof of the fourth ventricle is formed, and already we see the beginnings of the cerebellar hemispheres in the presence of two lateral outgrowths of nervous material known as the fimbria, which have already commenced to grow over and enclose these two lateral membranous bags.¹ By further growth the massive cerebellum of the mammalia is easily formed.

Striking, again, is it to see how the cerebral hemispheres of man have arisen from the simple cerebral lobes of *Ammocoetes* by the growth of nervous material over the original membranous pallium. In the accompanying diagrams the growth of this nerve mass is clearly seen, and also of the other dorsal nerve masses, until at last, by the formation of the human cerebral hemispheres, the corpora quadrigemina, and the cerebellum, all that remains of the original epithelial tube, which was at first the most important part of the roof of the brain, is tucked away to form the choroid plexuses, the roof of the fourth ventricle, and the lamina terminalis. In every respect we see that the formation of the brain of man from that of a brain like *Ammocoetes* has been brought about by the steady continuation of the same process by which the brain of *Ammocoetes* was, on my theory, formed from the brain of the arthropod ancestor.

PRINCIPLE 3.—Changes of function can arise when the new function coexists, perhaps subordinately, with the primary

¹ *Op. cit.*, *Jour. of Physiol.*, vol. x. p. 194, fig. 8, pl. xix.

function ; or coexists in another member of the same group, or in one of its larval forms.

Clearly my hypothesis is in accordance with this principle ; for, as far as the nervous matter of the brain goes, not only is there no change of function, but, on the contrary, a steady continuation of the same process has taken place in the formation of the vertebrate brain, of precisely the same character as has taken place to form the brain of the highest arthropods. The comparison of the genesis of the functions of the different parts of the brain agrees with and emphasises the conclusions deduced from the comparison of the genesis of the anatomical arrangement. The functions of the different parts of the central nervous system of annelids and arthropods have been studied not only by the older anatomists, who were all desirous of comparing the different parts of the brain of the arthropod and the vertebrate, but also by a number of physiologists of recent years. In my paper in *Brain*, I stated how this evidence was in agreement with my theory, and especially relied upon the observations of Ward¹ on the brain region of *Astacus*. Quite recently three papers have appeared on the subject:—(1) “On the physiology of the brain of Annelids,” by Maxwell;² (2) “Comparative researches on the functions of the central nervous system of Arthropods,” by Bethe;³ and (3) “On the differentiation of the inhibitory properties and the co-ordinating functions in the ganglionic chain of Decapod Crustacea,” by Celesia.⁴ These three papers contain a good representation of the literature of the subject, and lead, in conjunction with the previous papers of Ward, to conclusions which may be shortly expressed as follows:—

The nerve centres of Appendiculata were originally formed of paired pre-oral ganglion (composed of probably three pairs of fused pre-oral ganglia), and a number of separate paired post-oral ganglia, each pair of which were capable of acting on their own account, so that they might all be described as of equal function,—the only pair of superior function which possessed co-ordinating and regulating power over the others being the

¹ *Journ. of Physiol.*, vol. ii. p. 214, 1880.

² *Pflüger's Archiv*, vol. lxxvii. p. 263, 1897.

³ *Pflüger's Archiv*, vol. lxxviii. p. 449, 1897.

⁴ *Atti della Soc. Ligustica di Sci. Nat. e. Geograph.*, vol. viii., 1897.

pre-oral or supra-oesophageal. With, however, the concentration and cephalisation of the foremost ganglia of the post-oral chain to form the fused infra-oesophageal or prosomatic ganglion mass, a marked co-ordinating power over the actions of the lower ganglia of the post-oral chain is found in this fused mass, and the marked regulating action of the pre-oral ganglia is then found to be the regulation by their inhibitory power of this co-ordinating machinery.

Thus Maxwell found in the earthworm, where the cephalisation of the post-oral ganglia is very slight, a considerable spontaneity in the walking movements after removal of the supra-oesophageal ganglia,—a spontaneity which was not affected by removal of the first post-oral pair of ganglia. On the other hand, in *Nereis*, where the first post-oral ganglia are the concentrated prosomatic or mouth ganglia, the co-ordination and spontaneity of the walking movements visible after removal of the supra-oesophageal ganglia are distinctly due to the presence of this infra-oesophageal mass; and now the supra-oesophageal ganglia display marked inhibitory power over these infra-oesophageal co-ordinating centres, so that in *Nereis*, just as Ward had noticed for *Astacus*, incessant restless movements are seen when the supra-oesophageal ganglia alone are removed.

So, also, the experiments of Bethe on *Astacus* and other arthropods all confirm the previous dictum of Ward; that these fused prosomatic infra-oesophageal ganglia which supply the mouth parts with nerves possess a marked co-ordinating power over the walking movements, *i.e.*, over the nerve centres of the segments behind them, and that the supra-oesophageal ganglia have marked inhibitory power over these co-ordinating centres,—a power which leads to their regulation, and so to voluntary spontaneity of action.

Celesia has shown in *Astacus* that whereas, as already mentioned, the sub-oesophageal ganglia are the centres of co-ordination for the locomotion of the thoracic appendages, yet this method of regulation does not hold good for the swimming function of the abdominal appendages. Here, just as in the case of the lower worms, the separate abdominal ganglia possess within themselves their own centres of automatic action to a certain extent, and the only co-ordination of the action of swimming takes place from

the supra-oesophageal ganglia. Celesia concludes from his experiments that—

' The supra-oesophageal ganglia is the organ for the co-ordination in time, as Spencer supposes for the cerebral hemispheres of vertebrates, that is, "for co-ordination of the impressions of the past for the needs of the future," but it still retains in a high degree in the case of Astacus the power of co-ordination in space (function of swimming).

' As there is in evolution a tendency to constitute a single organ (the sub-oesophageal ganglia) for co-ordination in space, and to establish a differentiation between this and the organ for co-ordination in time (Spencer supposes the first to be in the cerebellum of vertebrates), it is probable that, as a consequence of further differentiation, the centre of co-ordination for swimming will descend into the sub-oesophageal ganglion, the cerebrum remaining purely the seat of sensory and psychical phenomena.'

The evidence then shows that—

1. The supra-oesophageal or pre-oral ganglia of the higher arthropods are strictly comparable to the pre-chordal or fore-brain region of the Vertebrata, not only in their connection with special olfactory and optic sense organs, but also in their rôle as leaders, and in their inhibitory power over lower ganglionic centres.

2. The fused prosomatic or mouth ganglia, which are connected with the supra-oesophageal by the oesophageal commissures, are strictly comparable with the trigeminal or pre-otic part of the epichordal brain region of the vertebrate, connected, as it is, with the prechordal region by the crura cerebri, not only in their connection with the nerves of the prosomatic appendages and segments, but also because this part of the brain mass acts especially as a great co-ordinating and equilibrating centre,—a centre which, though subordinate to the supra-oesophageal ganglia, enables the animal to perform co-ordinated gait movements, to recover its balance when upset, etc., after the supra-oesophageal ganglia have been removed. Here, then, in the corresponding region of the vertebrate brain we find in *Ammocoetes* that the trigeminal group supplies not only the remnants of the prosomatic appendages, but from this region also is the starting-point of the cerebellum and the posterior corpora quadrigemina.

We see indeed how steadily the growth of a marked co-ordinating and equilibrating mechanism can be traced without a break from the commencing concentration of the prosomatic or mouth ganglia in the worms, up to the mighty masses of the cerebellum and corpora quadrigemina in man.

Finally, we have to consider the function of the fused mesosomatic ganglia. These ganglia, which are often called thoracic, and were originally separate, supply, in a large number of the Arthropoda, appendages which are used for walking or swimming. In many cases these appendages carry the respiratory branchial apparatus. Thus in *Limulus* the mesosomatic appendages are largely branchial, though still retaining swimming functions; while in the scorpion group all sign of locomotor function has gone, and the respiratory function alone remains.

The observations of Miss Hyde¹ have shown that each separate pair of mesosomatic ganglia in *Limulus* can act as an independent respiratory centre for its own pair of branchial appendages, and that the mesosomatic ganglia together act as an automatic respiratory centre, independently of either the prosomatic or supra-oesophageal ganglia. As already mentioned, by the concentration of more and more of these ganglia, and their fusion with the prosomatic ganglia, the medulla oblongata of *Thelyphonus* is formed; and we may feel certain, judging from the experiments on *Limulus*, that an automatic respiratory centre is situated within it, which can act independently of either the prosomatic or supra-oesophageal ganglia.

In absolute accordance with this, we see that in *Ammocoetes*, and indeed in all vertebrates, the vagus or post-otic part of the epichordal brain region, usually called the medulla oblongata, not only gives rise to the nerves which supply the branchial chamber, but contains the automatic centre of respiration.

Also, from the very fact that the respiratory act was, in the first instance, brought about by the movement of limbs which were used for locomotion, it follows that such movement was under the control of the supra-oesophageal ganglia, and therefore that respiration is not only automatic, but can be voluntary as well.

¹ *Journ. of Morphology*, vol. ix. p. 431, 1894, "The Nervous Mechanism of the Respiratory Movements in *Limulus Polyphemus*."

Further, we see from the observations of Ward and Celesia that, just as the supra-oesophageal ganglia or cerebrum possesses a controlling regulating power over the action of the infra-oesophageal ganglia in *Astacus*, which is especially manifested as constant inhibitory action, so also the infra-oesophageal ganglia possess a controlling inhibitory power over the activities of the next group of ganglia,—over, therefore, the activities of the mesosomatic ganglia,—which, as we have seen in *Limulus* and its allies, include the action of the respiratory centres.

It is, to my mind, significant, and in accordance with these observations, to find that in the higher vertebrates, according to the observations of Kronecker and Marckwald, the regulation of the respiratory centre is effected, not only by means of inhibitory influences passing from the lungs by way of the vagus nerves (Hering—Breuer automatic regulation), but also, when the vagi are cut, by means of inhibitory influences passing from the posterior corpora quadrigemina and the region of the trigeminal nucleus. In other words, just as has been observed in the arthropod, the co-ordinating centres in the prosomatic ganglia, *i.e.* the posterior quadrigemina, regulate the activities of the mesosomatic ganglia, *i.e.* the respiratory centre, in the medulla oblongata by their special inhibitory power. Again, the well-known fact that the reflex excitability of the cord is increased after isolation, and that such reflex activity can be inhibited from the corpora quadrigemina, is, in all probability, another sign of the inhibitory power of the prosomatic ganglia over the lower centres.

The functional part, then, of the brain region of vertebrates is explainable by the steady growth and elaboration of the corresponding nervous parts in the Appendiculata; and if we now consider the non-nervous epithelial tube, we see here also that its characters are compatible with the hypothesis; for the alimentary canal of *Limulus* and the scorpions consists of a simple tube lined with epithelium, in which no special digestive organs are to be found,—the digestive function being confined to the so-called liver, which, with the generative glands, surrounds the central nervous mass and alimentary tube. These digestive glands, on my hypothesis, still remained outside the central nervous system, and did not therefore take part in the

formation of the vertebrate brain, so that the consideration of their fate does not come into the present argument, which is concerned only with the alteration of function of that part of the invertebrate alimentary canal which is included in the vertebrate brain. Clearly if, as I suppose, the closure of the old oesophagus took place in the infundibular region, the structure of the cephalic stomach and intestine would be exactly that represented by the simple epithelial lining of the central canal and the free epithelial membrane of the choroid plexuses: the only difference between the two structures would be that these cells in vertebrates are ciliated, while in arthropods they are lined by chitin. Such a difference is not either unlikely or unreasonable, seeing that cilia are found instead of chitin in the primitive arthropod *Peripatus*; that the worm-like ancestors of the arthropods almost certainly possessed a ciliated intestine; and finally, that the researches of Hardy and MacDougall¹ on the intestine of *Daphnia* point directly to the presence of a ciliated rather than a chitinous epithelial lining of the intestine in this animal,—all evidence pointing to the probability that in the ancient arthropod forms, derived as they were from the annelids, the intestine was originally ciliated, and not chitinous. It is from such forms that I suppose vertebrates to have sprung, and not from forms like the living king crabs, scorpions, *Apus*, *Branchipus*, etc. I only use them as illustrations, because they are the only living representatives of the great Archaic group from which the Crustacea, Arachnida, and Vertebrata all took origin.

PRINCIPLE 4.—Organs that are clearly rudimentary in the higher group must be derived from corresponding organs which are functional in the lower.

See, again, how perfectly Principle 4 holds good on my hypothesis; for we see how, in the whole group of arachnids and in *Limulus*, the old extinct sea-scorpions, *Eurypterus*, *Pterygotus*, etc., two or more median eyes existed, innervated from well-defined optic ganglia, and that in *Limulus*, according to Lankester, these eyes had already begun to lose their function. In precisely the same situation, as the very keystone of the edifice

¹ *Proc. Camb. Phil. Soc.*, vol. viii., 1893.

I am building, we find in *Ammocoetes* a pair of median eyes, one of which is conspicuous and well built, with an optic nerve arising from a most conspicuous part of the brain in this animal, called the ganglion habenulæ,—an eye which I have shown¹—and, later, Leydig² has come to the same conclusion—to be an eye of an arthropod type,—an eye which is, to all appearance, nearly as capable of function as that of *Limulus* itself. Passing upwards, we find this pineal eye more and more losing the evidence of its origin, its large conspicuous optic ganglion—the ganglion habenula—falling more and more into the background, until at last the ganglion habenula is perhaps recognisable as a few cells in the optic thalamus, and the median eyes have become the pineal gland, with its pigment still left as brain sand, and its supposed function in old days as the seat of the soul, and in more modern times as a part of the original œsophagus. The great and striking rudimentary organ of the brain, the pineal eye, harmonises in its history, its structure, and its position most perfectly with my theory; but is an absolutely fatal stumbling-block to any view, such as that of Dohrn, Patten, etc., which shifts ventral and dorsal surfaces, and is put on one side, and not explained by any other theory. Of all the numerous signposts which nature has left in the vertebrate to point out the path of evolution, the pineal eye is the most conspicuous and the most indubitable, and cannot, therefore, be put on one side, but must be considered.

As to the pituitary body, that also is explained in a simple manner; but as it does not belong to the brain, I will not deal with it here.

PRINCIPLE 5.—In phylogeny, we must look at the most elementary of the animals whose ancestors we seek.

Principle 5 asserts that in phylogeny we must look at the most elementary of the animals whose ancestor we seek; and Shipley argued against me that, firstly, I arbitrarily chose as my starting-point a vertebrate, viz., *Ammocoetes*, which was already some distance up in the scale, and that I ought to have taken

¹ *Op. cit.*, *Brain*, 1889, and *Quart. Jour. Micr. Sci.*, 1890.

² *Das Parietal Organ der Amphibien und Reptilien*, Frankfurt a. M., 1890.

Amphioxus and the larval tunicates; secondly, that if I replied to this point that Amphioxus and the tunicates were degenerate forms of an Ammocoetes-like vertebrate, then he would remind me that Ammocoetes itself was degenerate on the same grounds as Amphioxus and the tunicates.

This latter statement I am totally unable to accept, and fail to see any cogency in the arguments used. I have read through Dohrn's paper on the subject; and as far as I can see, the evidence of degeneration in the lamprey is based on one doubtful fact, and an unproved and most improbable hypothesis. The doubtful fact is that the lamprey is a parasite; the hypothesis is that it was descended from gnathostomatous fishes.

The charge of parasitism is brought against the lamprey because it is said to suck on to fishes and so obtain nutriment: it is, however, undoubtedly a free swimming fish; and when we see it coming up the rivers in thousands to reach the spawning-beds, and sucking on to stones on the way in order to anchor itself against the current, or holding on tightly during the actual process of spawning, it does not seem justifiable to base a charge of degeneration upon a parasitic habit, when such so-called habit simply consists in holding on to its prey until its desires are satisfied. If, of course, its suctorial mouth had arisen from an ancestral gnathostomatous mouth, then the argument would have more force.

Dohrn, however, gives absolutely no evidence of a former gnathostomatous condition either in *Petromyzon* or, in its larval state, *Ammocoetes*. He simply assumes that the Cyclostomata are degenerated fishes; and then proceeds to point out the rudiments of skeleton, etc., which they still possess. Every point that Dohrn makes can be turned round; and, with more probability, it can be argued that the various structures are the commencement of the skeletal and other structures in the higher fishes; and not their degenerated remnants. Just compare the life-history of the lamprey and of the tunicate. In the latter case we look upon the animal as a degenerate vertebrate, because the larval stage alone shows vertebrate characteristics; and when transformation has taken place, and the adult form reached, the vertebrate characteristics have vanished, and the animal, instead of reaching a higher grade, has sunk low in the scale, the central

nervous system especially having lost all semblance to that of the vertebrates. In the former case we see also that a transformation takes place, a marvellous transformation, characterised by two most striking facts: on the one hand, the resulting animal is more like a higher vertebrate, for, by the formation of new cartilages, its cranial skeleton can be compared with that of the higher forms, and the beginnings of the spinal vertebræ appear; by the formation of new nervous material, and by the formation of new nerves, its brain increases in size and complexity, so as to compare more closely with higher vertebrate brains; its eyes become functional, and its branchiæ are so modified simultaneously with the formation of the new alimentary canal in the cranial region that they now surround branchial pouches which are directly comparable to those of higher vertebrates. On the other hand, the transformation process is equally characterised by the throwing off of tissues and organs, one and all of which are comparable in structure and function with corresponding structures in the Arthropoda,—the thyroid of the *Ammocoetes*, the velum, the tentacles, the muco-cartilage, the tubular muscles, all these structures, so striking in the *Ammocoetes* stage, are got rid of at transformation. Here is the true clue. Here, in the throwing off of invertebrate characters, and the taking on of a higher vertebrate form, especially a higher brain, not a lower one, *Petromyzon* proclaims as clearly as is possible that it is not a degenerate elasmobranch, but that it has arisen from *Ammocoetes*-like ancestors, even though *Myxine*, *Amphioxus*, and the tunicates be all stages on the downward grade from those same *Ammocoetes*-like ancestors.

For these reasons it seems to me that Shipley's criticism does not hold good, and that it is perfectly legitimate to look upon the *Ammocoetes* form of *Petromyzon* as the most elementary vertebrate, from which, on the one hand, the higher vertebrates ascended, and, on the other hand, *Amphioxus* and the tunicates descended. And I am the more emboldened to take this view when I recall Rabl's remark at the close of his address on the "*Metamerie des Wirbelthierkopfes*," at the meeting of the German Anatomical Society at Vienna in 1892:—"Die Untersuchungen über die Entwicklung des Selachierkopfes haben die Hoffnungen, die man auf sie setzte, nicht erfüllt. Vielleicht wird

man mit der Untersuchung der Ganoiden und Petromyzonten mehr Glück haben." ¹

PRINCIPLE 6.—Any explanation of the origin of a higher group from a lower group must be confirmed by the study of the development in the higher group.

We come now to Principle 6, and it is on this principle that my opponents are inclined to take their final stand. My theory of the origin of the vertebrate brain, say they, is against the embryological unities, therefore it is not worth consideration. The central canal of the vertebrate nervous system cannot be the remains of an invertebrate alimentary canal, because it is formed from the epiblast, not from hypoblast; and the theory of the germinal layers is so well established and so fundamental that no amount of anatomical and physiological coincidences are worth consideration if they involve statements which are contrary to the germ layer theory. When I read Wilson's paper on the "Embryological Criterion of Homology," ² and see in the *Zoolog. Centralblatt*, 1897, No. 22, that Heider contributes a paper entitled "Ist die Keimblätter-lehre erschüttert"; when I find not only in Sedgwick's paper on Peripatus, but in Whitman's works and elsewhere that the idea is gaining ground that the embryo starts as a syncytium, I wonder to myself how long will it be before the germ layer theory becomes only of historical importance, and can in no way be regarded as a more important factor than anatomical and physiological coincidences? Wilson says, p. 122, "It is clear that we cannot successfully analyse the morphological aspect of development without further knowledge of its physiological aspect. I believe that until this knowledge is forthcoming the embryological criterion of homology must remain of relatively small value, and be held in subordination to the anatomical."

Heider, in the paper referred to, criticises the large number of recent papers which bring forward evidence more or less antagonistic to the germ layer theory, and comes to the conclusion that the strongest evidence against its universal acceptance is to

¹ *Anatom. Anzeiger*, 1892.

² Biological Lectures at Marine Biol. Lab. of Wood's Holl, 1894; Boston, 1895.

be found in the phenomena of budding, as especially seen in the Tunicata. Here the evidence is so concordant that the gut of the animal formed from the bud may arise from either ectoderm or endoderm, that it seems impossible that a mistake of observation can have occurred. In Wilson's paper the way in which the endoderm of the new bud is formed from ectoderm is well illustrated. So strong is this evidence, so difficult is it to bring the formation of the new gut in the phenomenon of budding into line with the germ layer theory, that Heider, who strongly advocates the retention of this theory for all direct embryological development, and thinks that the difficulties in connection with regeneration of lost parts will ultimately be explained in accordance with the germ layer theory, is obliged to confess, in respect to the phenomenon of budding, that, as far as we can see at present, the expectation that in this case also everything will finally be explained in favour of the germ layer theory must be looked upon as exceedingly small.¹

It is somewhat interesting, from my point of view, that the confusion between ectoderm and endoderm should have reached its maximum in the tunicate group, for upon my theory it is just in such a degenerate vertebrate group that one would expect to find such a confusion.

I myself stated, in my first paper in the *Journal of Physiology*,² that I intended to trace out all the coincidences possible, anatomically and physiologically, before discussing the embryological difficulties, feeling sure that the standpoint of embryological teaching would by that time have altered so much that many if not all of the difficulties would be found to have vanished. That was written ten years ago, and already my words are being verified.

Apart, however, from the question of the germinal layers, as Heymons³ has pointed out, ontogeny gives great value to phylogenetic speculations by the consideration of the manner in which the adult organ is gradually formed, and especially the time relations of the several stages of such formation. In other words, the further development of every organ in the vertebrate, after that organ has become differentiated, ought to be in harmony with the assumed line of ascent. Considered from this point of

¹ *Op. cit.*, p. 736.

² *Op. cit.*, p. 205.

³ *Die Embryonalentwicklung v. Dermapteren u. Orthopteren*, Jena, 1895.

view, and leaving for the present the consideration of the valency of the germinal layer theory, my theory of the origin of the vertebrate central nervous system is not only in harmony with the embryological developmental history of that system, but immediately explains in a simple and natural manner a number of embryological peculiarities of the central nervous system which have been hitherto absolutely unexplained.

On my theory, the central nervous system originated as a series of ganglia, connected by transverse commissures lying ventrally and laterally to the alimentary tube, which was free from nervous matter on its dorsal side, except in the region of the supra-oesophageal ganglia. This tube possessed a dilated anterior extremity—the cephalic stomach—which terminated in the oesophagus; and a straight part—the intestine—which terminated in the anus. By the subsequent growth of the nervous matter dorsally over this tube, the adult brain and spinal cord, with its central canal, were formed, and the free part of the tube which terminated in the anus was obliterated.

Is it possible for embryology to give a clearer indication of the phylogenetic steps which my theory necessitates than it does?

In my paper in the *Journal of Physiology*, 1889, I have pointed out how fully the study of the formation of the vertebrate nervous system in the embryo bears out the phylogenetic history according to my interpretation. I will refer my readers to that paper and to the paper in the *Quarterly Journal* for the full discussion, and will here simply sketch out the embryonic history.

When the tube of the central nervous system in the region of the spinal cord is first formed it is large, and the distinctly nervous tissue is seen at first forming two large lateral bulgings, the main part of which is situated on the ventral lateral half of this tube; very early, the anterior white commissures are formed, connecting these ventral lateral ganglion masses with each other, so that this stage represents the fused bilateral ventral chain of ganglia, together with their transverse commissures closely pressed against the alimentary tube on its lateral and ventral aspects. Next comes the dorsal spreading and growth of these nerve masses, by which the dorsal portion of the tube is compressed and obliterated to form the posterior fissure, and at the same time the same process of compression

obliterates the middle portion of the tube, and so, forms the posterior grey commissure and the substantia Rolandi. By this growth and compression the original large tube is converted into the small central canal of the adult in the spinal region. In the cranial epichordal region the same process takes place, with the difference that the original tube formed is here dilated, and so large that the ventral lateral ganglionic masses which represent the fused prosomatic and mesosomatic ganglia are able only to compress and grow over the ventral portion of this dilated tube, and by this compression form the raphé so characteristic of this region. Again we see how the dilated anterior extremity of the tube—*i.e.*, the old cephalic stomach—is divided into three and then into five cerebral vesicles by the formation of a series of constrictions, each one of which indicates the growth of nervous bands, and is the embryological expression of the commissural constrictions on the cephalic stomach caused by the connection between the supra-oesophageal ganglia, the optic ganglia, and the infra-oesophageal ganglia, by the crossing over of the fourth nerve, and the growth of the cerebellum. Thus the first three cerebral vesicles are formed by the growth of the cerebral hemispheres and the anterior commissure between the two hemispheres, by the posterior commissure between the optic parts and the epichordal brain, by the fourth nerve and the commencing cerebellum. Then come further constrictions, owing to the growth of the cerebrum and cerebellum, with the ultimate formation of the five cerebral vesicles, as pointed out in my paper in *Brain*. Not only does embryology show us step by step how the vertebrate nervous system has been formed by the steady growth of the arthropod nervous masses around the straight intestine and cephalic stomach, but it completes the evidence by showing that at one time of embryonic life, after that tube was formed, it passed free of the nervous material, to terminate as the neurenteric canal in the anus; while at the anterior end its termination is shown by the formation and presence of the infundibular canal coming to the surface of the brain between the two great oesophageal commissures, the crura cerebri.¹ Further, also, the

¹ It is worth noticing in this place that in the regenerated tail of the lizard, the central canal alone continues into the new formed tail, but there is no new formation of the spinal cord.

fusion of the separate ganglia to form the epichordal portion of the brain is shown embryologically, not only by the presence of the neuromeres, but also by the more evident manner in which the ganglion cells are grouped in separate masses in the embryo than in the adult.

I cannot see how it is possible to expect that ontogeny should recapitulate the phylogenetic history more perfectly than it does on my theory of the meaning of the tubular nature of the central nervous system: step by step it shows us how that nervous system was formed; and every part, both in time and nature, is in exact accordance with the requirements of my theory.

On the other hand, what aid does this embryonic history give to the phylogenetic speculations of others? On any of the other theories, why is there a nerve tube found with a dilated anterior extremity? why are the cerebral vesicles formed? why the choroid plexuses? why does that tube terminate in the anus? why is there an infundibular prolongation? What answer is given to these questions?

As we have seen, the opponents of the origin of vertebrates from the Appendiculata are forced to rely on the teachings of vertebrate embryology as their main guide to their phylogenetic speculations. From them surely we ought to expect an answer to these questions, and yet what do we find? On the one hand, speculations as to the manner in which a simple tubular nervous system may have been formed, without the slightest suggestion of how the complicated vertebrate tube, with all its peculiarities, has arisen. On the other hand, a simple begging of the question by that most convenient modern method of asserting that what cannot be explained is coenogenetic, and has no phylogenetic importance. Thus Ray Lankester, in his article on the "Vertebrata" in the *Encyclopædia Britannica*, p. 179, says: "The tubular condition of the cerebro-spinal nerve-cord of Vertebrata is now very generally regarded as being in its origin a purely developmental feature."

I have now shown how completely my theory of the origin of the brain of the vertebrate is in harmony with the six principles laid down, and in consequence it must at least be looked upon as a working hypothesis from which the origin of the rest of the vertebrate organs may be considered. Before, however, leaving

the consideration of the central nervous system and passing on to other organs, it is advisable to notice shortly the conclusions of those with regard to the central nervous system who do not recognise any near relationship between the Vertebrata and the Appendiculata. For this purpose I will take the latest paper on the subject, viz., that of Fürbringer,¹ and state the conclusions he has arrived at from his investigations into the nervous systems of the lower vertebrates; conclusions based especially upon the view that the nervous system of *Amphioxus* represents a primitive vertebrate type.

Fürbringer, at the end of his long paper on the "Spino-Occipital Nerves," in which he compares the cranial nerves of the various vertebrate groups with the nerves of *Amphioxus*, comes to the conclusion that the primitive chordate possessed—

1. A central nervous system, built up regularly in the same manner along the whole length of the body, formed as a dorsal median plate out of the ectoderm, and continuous laterally with the rest of the less highly differentiated ectoderm.

2. An unpaired chorda, lying under this in the middle line, and two paired mesodermal plates on both sides, which gave origin to the supporting, muscular, urogenital and vascular systems, and were connected with the central nervous system.

3. An alimentary canal lying under the chorda, also connected with the central nervous system.

The central nervous system became grooved, then by closure formed a canal, dividing at the same time into median motor and lateral sensory parts, which then became ventral and dorsal.

In the neighbourhood of the chorda the mesoderm plate (the Wirbelzone, epimere zone) differentiated into median longitudinal muscle bands, while the lateral mesoblast (Seiten-platten zone, hypomere zone) formed muscle fibres more in the transverse direction.

Then came metamerism by division of somatic muscles into somites, and to a less extent of visceral muscles into visceral myomeres; with this came metameric arrangement of the motor nerves, which hitherto had been indifferent in position.

Simultaneously with this evolution, a differentiation into head and body took place in the original elongated organism, which was up to that time exactly the same in all its parts, and then began the formation of specific sense organs, first for equilibration, smell and taste, and afterwards for sight and hearing. Also the anterior intestinal tube folded itself, with formation of successive openings, and became respiratory, and finally special armature for the mouth was formed.

¹ "Ueber die Spino-occipitalen Nerven der Selachier u. Holocephalen u. ihre vergleichende Morphologie," *Festschrift f. Carl Gegenbaur*, Leipzig, 1897.

We may sum up the differences between Fürbringer's view and myself in three propositions:—

1. I look upon the cranial region as the most primitive, and the spinal region as an after-thought.

He looks upon the cranial region as the outcome of the spinal.

2. I look upon the vertebrate as the direct descendant of the most markedly segmented of the invertebrate group.

He looks upon the chordate ancestor as being unsegmented.

3. The foundation upon which I build my ancestor is a central nervous system of the highest invertebrate type, even though the alimentary canal has to be formed anew in consequence.

His ancestor possessed a vertebrate notochord and alimentary canal when the nervous system was hardly differentiated.

We have therefore the three following criteria upon which to decide between these two opposing views:—

1. Is the cranial region older than the spinal, or *vice versa*?

2. Was the near ancestor of the vertebrate segmented or unsegmented?

3. Which is the most important factor in evolution—the central nervous system, or the alimentary canal?

The first of these three questions must be answered in favour of the origin from forms such as exist in the Appendiculata, rather than from an *Amphioxus*-like animal, for the following reasons:—

The evidence of embryology points directly to the greater phylogenetic antiquity of the cranial region; for we see how early in the history the head is folded off, and thereby the organs in that region are completed at a time when the spinal region is only at an early stage of development; we see how the first of the trunk somites is formed just posterior to the head region, and then more and more somites are formed by the addition of fresh segments posteriorly to the first formed one; we see how in *Ammocoetes* the first formed parts of the skeleton are the branchial bars and the basi-cranial system, while the rudiments of the vertebræ do not appear until the *Petromyzon* stage; we see how, with the elongation of the animal by the later addition of more and more spinal segments, organs such as the heart, which were originally in the head, travel down, and the vagus and lateral line nerves reach their ultimate destination.

Again, we see that, whereas the anterior cranial nerves, the eye nerves, the trigeminal, facial, auditory, glosso-pharyngeal and vagus are wonderfully fixed and constant in all vertebrates, the only shifting being in the spino-occipital region, in fact at the junction of the

cranial and spinal region, the spinal nerves, on the other hand, are not only remarkably variable in number in different groups of animals, but even in the same animal great variations, especially in the manner of formation of the limb plexuses, are found. Such marked meristic variation in the spinal nerves, in contrast to the fixed character of the cranial nerves, certainly points to a more recent formation of the former nerves.

Again, the observations of Assheton¹ on the primitive streak of the rabbit, and on the growth in length of the frog embryo, have led him to the conclusion that, as in the rabbit so in the frog, there is evidence to show that the embryo is derived from two definite centres of growth: the first, and phylogenetically the oldest, being a protoplasmic activity which gives rise to the anterior end of the embryo; the second, which gives rise to the growth in length of the embryo.

This secondary area of proliferation coincides with the area of the primitive streak; and he has shown in a subsequent paper,² by the insertion of sable hairs into the unincubated blastoderm, that a hair inserted at the centre of the blastoderm appears at the anterior end of the primitive streak, and, subsequently, is found at the level of the most anterior pair of somites. He then goes on to say, p. 353: "From these specimens it seems clear that all those parts in front of the first pair of mesoblastic somites (that is to say, the heart, the brain, and medulla oblongata, the olfactory optic and auditory organs and foregut) are developed from that portion of the unincubated blastoderm which lies anterior to the centre of the blastoderm, and that all the rest of the embryo is formed by the activity of the primitive streak area." In other words, the secondary area of growth, *i.e.*, the primitive streak area, includes the whole of the spinal cord region: while the older primary centre of growth is coincident with the cranial region.

I fail to see any evidence that the cranial region has been derived from the spinal, while the evidence is consistent and strong that the embryo has grown in length by the addition of segments in regular sequence behind the first formed cranial region.

The answer to the second question must undoubtedly be in favour of the origin from a segmented ancestor, and therefore in favour of the origin from the Appendiculata.

Both in the adult and in the embryo vertebrate, the evidence of segmentation is confessedly very strong; and I imagine that no doubt on the question would have arisen if it were not for the unsegmented notochord and unsegmented tubular formation of the central nervous system. In fact, as we see, Fürbringer's primitive chordate possessed an unsegmented alimentary canal, an unsegmented notochord, and an

¹ *Quart. Jour. of Micros. Sci.*, pp. 191 and 223, 1894.

² *Proc. of Roy. Soc.*, vol. lx., p. 349, 1896.

unsegmented central nervous system. Undoubtedly the manner in which the tubular nervous system is formed has always been a strong argument in the minds of those who hold the view of the origin of vertebrates from an unsegmented ancestor, and the impossibility, therefore, of origin from a nervous system so markedly segmented as is characteristic of the Appendiculata. My theory removes this objection in the simplest and most complete manner, for even in the most segmented animals the alimentary canal is unsegmented; therefore, naturally, the vertebrate nervous system, formed as it is of the conjoined nervous system and alimentary canal of the appendiculate ancestor, is formed of an unsegmented part, the central canal, and a segmented part, the nervous material proper; and, equally naturally, the formation of the unsegmented tube is the most striking part of the nervous system when first formed, although recent researches (see especially Locy's paper) have brought to light a regular segmentation in the nervous system, even before the tubular canal is fully formed.

Fürbringer's three characteristics, then, of the unsegmented ancestor, the alimentary canal, the tube of the nervous system, and the notochord, are all explained on my theory in the same way; they are all unsegmented for the same reason, viz., that at one time or another they functioned as an alimentary canal, and therefore were unsegmented, even though the rest of the animal was of the most marked segmental type. A very striking instance of the manner in which an unsegmented alimentary canal is formed in a markedly segmented region is seen in the case of the formation of the new gut in the cranial region at the transformation of *Ammocetes* into *Petromyzon*, where an absolutely unsegmented tube is formed, although the hyperpharyngeal ridge, from the proliferation of some of the cells of which the solid cord is formed, which then hollows out to form the gut, is markedly segmented in connection with the branchiæ.

The answer to the third question, to my mind, must be in favour of the paramount importance of the central nervous system, especially the front part of it, or brain.

The central point of my theory, which places the vertebrate ancestor in the appendiculate group, is the close resemblance between the brain of the *Arachnida* and of the *Ammocetes*; and it follows that, on my theory, the dominant factor of the evolutionary process, whereby higher forms and groups of animals are developed from lower, is the steady increase of brain power, regardless of the question whether the alimentary canal is thereby altered.

The history of evolution, as far as it is known, certainly appears to bear out the conclusion that the *ego* of the individual lies in the brain, and not in the alimentary canal; that whatever changes take place in the other organs, the question whether any metamorphosis will produce a lower or a higher form depends upon whether the brain is involved in that metamorphosis or not; that in all great groups of

animals the striking difference between the highest and lowest of that group is the difference in size of the brain. Thus the manifest distinction between the lowest fish and the highest mammal is the marked increase in size of brain and in brain power. The same law applies to the difference between the lowest and the highest mollusc, the lowest and the highest of the great appendiculate group.

It is therefore clear that, in order to form the lowest of the higher group of Vertebrata, the invertebrate ancestor must have possessed a brain very slightly inferior to that of such lowest vertebrate. Is there the same necessity that the alimentary canal should always remain the same?

The paramount importance of the central nervous system over the other organs, the leading rôle which it plays, is exemplified in the metamorphosis of insects and of the lamprey. In both cases, throughout the changes which take place, the central nervous system steadily increases in size and in complexity; in the former case the separate ganglia of the larva concentrate and fuse together especially in the thoracic and head regions, as was well shown by Newport¹ in 1832 and 1834. The process of histolysis by which the larval tissues of the insect are destroyed, and then from the imaginal discs the new organs of the adult are formed, leaves the central nervous system alone intact; or, at all events, the loss of the elements of the central nervous system which is associated with the destruction of the larval tissues is rendered unapparent by the concomitant growth of the new elements of the nervous system formed for the innervation of the new tissues of the adult, or perhaps one might even say responsible for the growth of those new tissues. During the time, then, of the histolysis and rebuilding, when there is no trace of a functional alimentary canal, the central nervous system is still intact, still regulating and controlling the metabolic processes so actively taking place.

Most striking, again, is the transformation process by which the *Ammocoetes* is converted into a *Petromyzon*. Here also a process of histolysis takes place, which affects the whole of the cranial region of the animal except its central nervous system. All the organs in the branchial and oral chambers are flooded with blood, many of their tissues utterly destroyed, and for a time, the length of which is unknown, but must certainly be reckoned by weeks, and probably by months, the alimentary canal is functionless, for the solid rod of cells which afterwards hollows out and forms the new gut in this region closes entirely the entrance to the intestine from the branchial chamber, so that until the lumen, which begins at the caudal end, is formed through the whole length of the rod, the only possibility of taking in food is afforded by the respiratory chamber itself. During the whole of this time the brain region remains intact, no change having taken place in it except increase of growth and power. So clear to my mind is the paramount importance of the increase of brain power for all upward evolution, that I cannot doubt but that if an antagonism takes place between the alimentary canal and the central

¹ "On the Nervous System of the *Sphinx Ligustri*," *Phil. Trans.*, 1832 and 1834.

nervous system, the upward evolution will belong to that group in which the latter has gone on steadily growing, even though thereby new digestive arrangements may have been necessitated.

Having, then, cleared the ground so far, it follows that if my theory is true, its confirmation must be sought for, in the first instance, in the details of the anatomy of the cranial region, and that, therefore, an explanation of the meaning of the distribution and function of the segmental cranial nerves must first be sought for.

For this purpose I determined to examine the head region of *Ammocoetes* thoroughly from a different point of view to that of my predecessors: whereas they had looked at its structure in order to compare it with other vertebrates, keeping in mind especially the possibility of its being a degenerated form, I determined to look at its structure in order to compare it with invertebrates, keeping in mind especially the possibility of its being a modified arthropod. The fact of its being a larval form, with a long free living existence before transformation takes place and it becomes a full grown *Petromyzon*, made it especially favourable for my purpose; for the great importance of such a factor in tracing back an ancestral form is universally recognised, and has been especially emphasised by Sedgwick¹ in his paper on the "Law of Development known as von Baer's Law," in which he concludes that, "whereas larval development must retain traces of ancestral stages of structure because they are built out of ancestral stages, embryonic development need not necessarily do so, and very often does not; that embryonic development, in so far as it is a record at all, is a record of structural features of previous larval stages."

The conclusions to which the study of the head region of *Ammocoetes* as a modified Arthropod led me were, that the cranial nerves in this animal innervated structures and organs which could without difficulty be derived from an Arthropod type, especially such a type as *Eurypterus*; and I came to the conclusion that the remains of *Eurypterid* appendages were still existent in *Ammocoetes*, and that the cranial nerves owed their peculiarities to their innervation of such appendages. Such innervation divided itself naturally into the two great groups

¹ *Quart. Jour. of Microsc. Sci.*, vol. xxxvi.

emphasised by Gegenbaur, which may be called the Trigeminal and Vagus groups: such groups corresponded respectively, according to my theory, with the prosomatic and mesosomatic nerve-groups of Eurypterus; of which the former, as in Ammocetes, innervated the appendages of an oral chamber, while the latter innervated the appendages of a branchial chamber. The remnants of prosomatic appendages in Ammocetes were the tentacles and velum, while the appendages of the branchial chamber were the branchiæ and thyroid gland and their supports.

It seemed to me a very strong reason for supposing that I was on the right line of research to find that all these very structures and organs which I had thus interpreted as ancestral remnants either absolutely disappeared or were greatly modified when the metamorphosis takes place. Away go tentacles and velum, away goes thyroid, a new gut is formed in the cranial region, and the branchial chamber is so altered as to be capable of description in the ordinary term of gill pouch and gill slit. Especially, too, is it noticeable that every trace of muco-cartilage and of the tubular muscles disappears, that the black pigment under the skin becomes white, and the laminated layer of the dermis is altered in character. In fact, a number of tissues and organs are got rid of in the cranial region, every one of which, on my theory, plainly indicates its past invertebrate history.

The conclusion to which I had thus come, that a type more or less similar to that of Eurypterus was the most likely to give a clue to the origin of these various structures in Ammocetes, led me to examine the tissues and organs of Limulus and the scorpion tribe as the only existing animals which could be expected to throw light on the internal structure of Eurypterus and its allies. As I have pointed out in my Liverpool address, my hopes and expectations were gratified to the full; for not only did I find that peculiarities of the cranial nerves were easily referable to the arrangement of the nerves in the scorpion and Limulus group, that the muco-cartilage and the peculiar cartilage of Ammocetes were present in the same position and of the same structure in Limulus, that the peculiar thyroid gland has its counterpart in the corresponding position in the scorpion, but also, by arguing in the reverse direction, I was able to find the unknown auditory and olfactory organs of these animals, for the

flabellum of *Limulus* fitted in with the auditory sac of *Ammocoetes*, and the camerostome of *Thelyphonus* seemed to be the exact homologue of the olfactory organ of *Ammocoetes*.

Such, then, appears to me to be the most certain method of finding out the nature of the ancestor of the vertebrates: in the first place, to study up to the minutest detail the anatomy and the physiology of *Ammocoetes*, and in this way to obtain more and more points of comparison between it and its presumed arthropod ancestor. There is only one scientific way of finding out the past history of the vertebrate, and that is to interrogate the vertebrate itself.

I propose then, in this and the following papers, to take the tissues and organs of the *Ammocoetes* one by one and compare them with those tissues and those organs in *Limulus* and the scorpion group with which, on my theory, they are homologous. I will leave further consideration of the central nervous system for the present, and proceed in my next part to the consideration of the cartilaginous skeleton of the head region.

PART II.—THE ORIGIN OF THE VERTEBRATE CRANIO-FACIAL CARTILAGINOUS SKELETON.

In the consideration of the central nervous system we saw that we could trace back step by step every part of the brain (through the *Mammalia*, *Aves*, *Reptilia*, *Amphibia*, *Petromyzon*) down to the simple brain of *Ammocoetes*; so also, in considering the origin of the vertebrate cranio-facial skeleton, we find similarly that it can be traced back step by step to the cartilaginous skeleton of the *Ammocoetes*.

The axial skeleton of man consists of two parts:—

1. The vertebral column, with its attached bony parts, all of which are formed from cartilage.
2. The cranio-facial skeleton, partly formed from cartilage, partly from membrane.

In the early part of this century the cranio-facial skeleton was supposed to be formed of a number of modified vertebræ. This theory was overthrown by Huxley in 1869, who showed that the true evidence of segmentation in the head region was obtainable

from the cranial nerves and the branchiæ, and not from the study of the superficial sutures in the cranium. From this time until now it has become more and more certain that the cranio-facial skeleton cannot be explained as a number of modified vertebræ, but rather as formed of skeletal structures, which arose, in the first instance, in connection with the visceral and branchial arches.

If we trace back its formation we see, as we pass through the reptiles to the amphibians and fishes, how clearly the facial skeleton of the mammals can be traced back to the modification of a series of visceral and branchial arches. Especially neat and instructive is the history of the modifications by which the ear bones have arisen, so that, as we see from the series of monographs by Parker, we can trace back the bony skeleton of the head to that of the tadpole of the amphibian, and the great group of fishes. Further, Parker has shown that the cartilaginous cranio-facial skeleton of *Petromyzon* is distinctly comparable with that of the tadpole, so that the cranio facial bony skeleton of the higher Vertebrata can be derived directly from a non-bony cartilaginous skeleton, such as is seen in *Petromyzon* and the cartilaginous fishes. Such skeleton consists essentially of a series of visceral and branchial cartilaginous bars, together with the basal trabeculæ and parachordals, and a cartilaginous unsegmented cranium, to which must be added auditory and nasal capsules. But *Petromyzon* is derived from *Ammocoetes* by a remarkable process of transformation, and a most important part of that transformation is the formation of new cartilaginous structures. Thus we see that in *Ammocoetes* there is no sign of a cartilaginous vertebral column: at transformation the rudimentary vertebræ of *Petromyzon* are formed. In *Ammocoetes* the brain-case is a simple fibrous membranous covering; at transformation this becomes cartilaginous: there are no cartilaginous structures in the anterior part of *Ammocoetes* corresponding to the sub-ocular arches. These are all formed at transformation: it follows, therefore, that we can trace back the bony skeleton of the vertebrate head to the skeleton of *Ammocoetes*, and we may therefore conclude that the primitive cartilaginous skeleton of the vertebrate consisted of the following structures (fig. 5B), viz., the branchial bars forming a basketwork, the trabeculæ and

parachordals, the auditory and nasal capsules,—a clear proof, if more were wanted, that the cranial skeleton is older than the spinal. Of these structures the branchial bars are the only clearly segmented parts.

If, then, my hypothesis will explain the origin of these parts, it will explain at the same time the origin of the whole of the bony skeleton of the vertebrate head.

On the Topographical Arrangement of the Soft Cartilage of the Branchial Skeleton of Ammocetes.

The study of Ammocetes shows us that its skeletal parts fall naturally into two marked groups, characterised by a difference in the structure of the cartilage, by a difference in topographical position, and by an independence of origin.

These two groups are the branchial and the basi-cranial groups respectively. J. Müller¹ was the first to point out that these two sets of cartilages differed in appearance and constitution, and he gave to them the name of yellow and grey cartilage. Parker² has described them fully under the terms soft and hard cartilage, terms which Schaffer has also used, and I shall also make use of them in this paper. We see, as is shown in fig. 5B, that the whole of the branchial cartilaginous skeleton is composed of soft cartilage, while the basi-cranial skeleton, consisting of trabeculæ, parachordals, and auditory capsule, is composed of hard cartilage, the only soft cartilage in this region being that which forms the nasal capsule not represented in the figure.

Further, we see that these two groups of cartilage arise independently, so that at first the basi-cranial system is quite separate from the branchial, and only late in the history of the animal is a junction effected between the branchial system and the trabeculæ and parachordals,—an original separation which is especially striking when we consider that in this animal all the cartilaginous structures of any one system are continuous: there is no sign of anything in the nature of joints.

Of these two main groups, the branchial cartilages are first

¹ "Vergleich. Anat. d. Myxinoiden," *Abhandl. d. Kgl. Akad. d. Wiss.*, Berlin, 1834.

² "On the Skeleton of the Marsipbranch Fishes," *Phil. Trans.*, 1883, p. 411.

formed embryologically, a fact which suggests that they are the most primitive of the vertebrate cartilages, and that, therefore, the first true formation of cartilage in the invertebrate ancestor may be looked for in the shape of bars supporting the branchial mechanism. The evidence of the origin of the carti-



FIG. 5.—Comparison of Cartilaginous skeleton of *Limulus* and *Ammocoetes*.

- A, diagram of cartilaginous skeleton of *Limulus*. *Soft cartilage*—Entaphophysial ligaments, deep black; branchial bars, simply hatched. *Hard cartilage*—Lateral trabecule of entosternite, netted. *Ph*, position of pharynx.
 B, diagram of cartilaginous skeleton of *Ammocoetes*. Sub-chordal cartilaginous bands, deep black; branchial basket work (first formed part), simple hatched; craniofacial skeleton trabeculae and auditory capsules, netted. *Inf*, position of tube of infundibulum (old oesophagus).

laginous structures in *Ammocoetes* is given by Shipley¹ in the following words:—

“The branchial bases are the first part of the skeleton to appear. They arise about the 24th day as straight bars of cartilage, lying

¹ *Quart. Jour. of Micros. Sci.*, 1887.

external and slightly posterior to the branchial vessel. In their relation to the vessel they correspond with the extra-branchial bars of the tadpole and the sharks.

"The first traces of the basi-cranial skeleton appear on the 30th day as two rods of cartilage—the trabeculae."

Our attention must, in the first place, be directed to this branchial basketwork of *Ammocoetes*.

This branchial skeleton has been so often described before, and quite recently again by Schaffer,¹ that it is unnecessary to re-describe it. Parker gives its general appearance in the adult *Petromyzon* in figs. 1 and 2, pl. xviii. We see that it is simpler in *Ammocoetes* than in *Petromyzon*, and that its actual starting-point consists of a main transverse bar corresponding to each branchial segment; from this transverse bar the system of longitudinal bars by which the basketwork is formed has sprung. These transverse bars arise from a cartilaginous longitudinal rod, situated close against the notochord on each side. These rods may be called the subchordal cartilaginous bands; and, according to the observations of Schneider² and others, each subchordal band does not form at first a continuous cartilaginous rod, but the cartilage is conspicuous only at the places where the transverse bars arise. In the youngest *Ammocoetes* examined by Schaffer, he could find no absolute discontinuity except between the first two transverse bars, but he says that the thinning between the transverse bars was so marked as to make it highly probable that at an earlier stage there was discontinuity. The whole system of branchial bars and subchordal rods is at first absolutely disconnected from the cranial system of trabeculae and parachordals, and only later do the two systems join.

We see, then, that the observations on *Ammocoetes* lead most definitely to the conclusion that the starting-point of the whole cartilaginous skeleton of the vertebrate consisted of a series of transverse cartilaginous bars, for the purpose of supporting branchial segments, which were connected with two axial longitudinal cartilaginous rods, which at first contained cartilage only near the places of junction of the branchial bars.

In addition to this primitive cartilaginous framework, which

¹ *Zeitschr. f. Wissen. Zool.*, vol. lxi. p. 606, 1896.

² *Beiträge z. Anat. u. Entwicklungsgesch. der Wirbelthiere*, Berlin, 1879.

was formed for the support of the mesosomatic or respiratory segments, but at a slightly later period in the phylogenetic history, a separate cartilaginous system was formed for the support of the prosomatic segments, viz., the trabeculæ and parachordals with the auditory capsules: a system which was at first entirely separated from the mesosomatic, and, as we shall see, is more advanced in structure than the branchial system. Later still, the story is completed at the time of transformation by the formation of the simple cartilaginous skull and the rudimentary vertebræ, the structure of which is also of a more advanced type.

So much for the topographical position of the original cartilaginous skeleton. Before, however, we can form a conception of the origin of these branchial cartilaginous bars, we must know also their structure, and see how such structure has arisen.

On the Structure of the Branchial Cartilages in Ammocetes.

In the higher vertebrates various forms of cartilage are described, viz., hyaline, fibro-cartilage, elastic-cartilage, and parenchymatous cartilage. Of these, the parenchymatous cartilage is looked upon as the most primitive form, because it preserves without modification the characters of embryonic cartilage.

Embryology, then, would lead to the belief that the earliest form of cartilage in the vertebrate kingdom ought to be of this type, viz., large cells, each of which is enclosed in a simple capsule, so that the capsules of the cells form the whole of the matrix, and form a simple homogeneous honeycomb structure, in the alveoli of which the cartilage cells lie singly. If, then, the branchial cartilages of Ammocetes are, as has just been argued, the representatives of the cartilaginous skeleton of the primitive vertebrate, it is reasonable to suppose that they should resemble in structure this embryonic cartilage. Such is undoubtedly the case: all observers who have described the branchial basketwork of Ammocetes or Petromyzon have been struck with the extremely primitive character of the cartilage, and the last observer (Schaffer) described it as composed of thin walls of homogeneous material, in which there are no lines of separation, which form a simple honeycomb structure, in the alveoli of which the separate cells lie singly. These branchial cartilages are each surrounded

by a layer of perichondrium, and in fig. 1, Pl. XIII., I give a picture of a section of a portion of one of the bars and its perichondrium.

Hence we see that structurally as well as topographically the branchial bars of *Ammocoetes* justify their claim to be considered as the origin of the vertebrate cartilaginous framework.

On the Structure of the Muco-Cartilage in Ammocoetes.

We can, however, go further than this, and ask how this cartilage itself is formed in *Ammocoetes*? The answer is most definite, most instructive and suggestive; for we see that in all cases this particular kind of cartilage is formed from, or at all events in, a peculiar fibrous tissue, which was called by Schneider "Schleim-Knorpel," or muco-cartilage,—a tissue which is distinguishable from other connective tissues, not only by its structural peculiarities, but also by its strong affinity for all dyes which differentiate mucoid or chondro-mucoid substances.

This muco-cartilage is thus described by Schneider:—The perichondrium in *Ammocoetes* is not confined to the true cartilaginous structures, but extends itself in the form of thin plates in definite directions. Between these plates of perichondrium a peculiar tissue—the muco-cartilage—exists, consisting of fibrillæ, whose direction is mainly at right angles to the planes of the perichondrial plates, with star-shaped cells in among them, and with the spaces between the fibrillæ filled up with a semi-fluid mass.

From this tissue all the primitive cartilages which resemble the branchial bars are formed, either by the invasion of chondroblasts from the surrounding perichondrium, or by the proliferation and encapsulation of the cells of the muco-cartilage itself.¹

Before we can understand the formation of cartilage in *Ammocoetes*, it is clearly most important to map out the distribution of this peculiar tissue. In order to do this I made use of the micro-chemical reaction of thionin, a dye which, as shown by Hoyer,² stains all mucin-containing substances a bright purple. I found with this dye that the matrix or

¹ *N.B.*—I do not propose here to lengthen this paper by discussing the question whether the soft cartilage is always formed by means of chondroblasts which invade the muco-cartilage from without. I hope in a future paper to discuss the whole question of the formation of both soft and hard cartilage as shown at the time of transformation.

² *Archiv f. Microsc. Anat.*, vol. xxxvi., 1890.

ground substance of the branchial cartilages stained a deep purple, and that the matrix or semi-fluid substance in which the fibrils of the muco-cartilage are imbedded was also coloured deeply purple, while the fibrous material of the cranial walls and other connective-tissue strands were coloured light blue. In fig. 1, Pl. XIII., the manner in which the branchial cartilages are differentiated by thionin is shown, and in fig. 3 a portion of muco-cartilage, in which the formation of new cartilage is taking place, is coloured as it appears when stained with thionin. In this way it was easy to map out the distribution of this tissue more thoroughly than had been done by Schneider and Kaensche. Accordingly, in the paper which I sent to the *Quarterly Journal of Microscopical Science* in 1895, but which was never published, I gave such a description. As, however, Schaffer in his paper has mapped out this tissue by means of a corresponding stain—hæmalum—it is unnecessary for me to go into any detailed description of the position of these muco-cartilaginous plates, especially as I agree with his description. I will therefore confine myself to a very general description of its area of distribution.

In the first place, it is confined absolutely to the head region of *Ammocoetes*: no sign of it exists in other parts.

In the second place, it is not found in *Petromyzon* or the higher vertebrates: it entirely disappears at transformation, being eaten up by phagocytes, or else transformed into cartilage,—a fact of great significance, as pointing distinctly to an ancestral origin for this tissue.

In the third place, if we anticipate a future chapter, its distribution may be described as a series of muco-cartilaginous plates and bars in connection with the remnants of the prosomatic and mesosomatic appendages of the *Eurypterus*-like ancestor of *Ammocoetes*.

These may be tabulated as follows:—

Mesosomatic.—1. The plates of the branchial appendages, represented in *Ammocoetes* by the muco-cartilages of the branchial and subchordal cartilages.

2. The plates of the opercular appendages, represented in *Ammocoetes* by the median plate of muco-cartilage over the thyroid gland, together with its dorsal continuation along the line of the pseudo-branchial groove on each side.

Prosomatic.—1. The plate of the metastoma, represented in *Ammocoetes* by the plate of muco-cartilage of the lower lip.

2. The plate of the hypostoma, represented in *Ammocoetes* by the muco-cartilage of the upper lip.

3. The muco-cartilaginous plates of the prosomatic appendages, represented in *Ammocoetes* by the muco-cartilages in connection with the velum and the tentacles.

The conclusions to which we are led by the study of the structure, position, and mode of origin of these primitive cartilages of *Ammocoetes* may be thus summed up:—

1. The immediate ancestor of the vertebrate must have possessed a peculiar fibrous tissue—the ground substance of which stained deep purple with thionin—in which cartilage arose.

2. The cartilage so formed was not like hyaline cartilage, but resembled in a striking manner parenchymatous cartilage.

3. This cartilage was situated partly in two axial longitudinal bands, partly as transverse bars, which supported the branchial apparatus.

*On the Topographical Arrangement of the Soft Cartilage
of the Branchial Skeleton of Limulus.*

To such a conclusion the investigation of *Ammocoetes* alone had led me in 1890 when I published my paper in the *Quarterly Journal*. Consequently, I determined to search the literature of the histology of the cartilaginous tissues in invertebrate animals, and see whether any cartilage had been described similar to that seen in the branchial cartilages of *Ammocoetes*, and whether such cartilage, if found, arose in a fibrous tissue resembling muco-cartilage. My search was speedily rewarded by finding in Ray Lankester's article on the tropho-skeletal tissues of *Limulus*¹ a picture of the cartilage of *Limulus* which would have done for a drawing of *Ammocoetes* cartilage.

This tissue in *Limulus*, which was described by Gegenbaur² as cartilage in 1858, is called by Lankester capsuligenous connective tissue, and is described by him as formed in a peculiar fibrous

¹ *Quart. Journ. of Micros. Sci.*, vol. xxiv. p. 129, 1884, pl. xi. fig. 4.

² "Anatomische Untersuchung eines *Limulus*," *Abhandl. d. Naturforsch. Gesellschaft zu Halle*, Bd. iv., 1858.

tissue, which he considers to be of the same kind as that forming the fibrous material of the ento-sternite, to which he gave the name of fibro-massive tissue. This peculiar cartilage or capsuligenous tissue occurs, according to Lankester, in one special organ of *Limulus* only, and is not found elsewhere in that animal or at all in *Scorpio*. On each side of the mid-dorsal line in the abdominal carapace a series of invaginations of the chitinous covering, corresponding to the mesosomatic segments, are seen in *Limulus*; the inward massive projections of chitin thus formed are called entapophyses, and Lankester found that each entapophysis is connected with its neighbour by a ligament which was composed of fibro-massive tissue, with an axial core of this peculiar cartilage, so that there is formed on each side of the mid line an entapophysial ligament, more or less cartilaginous in nature. At each entapophysis the cartilage is described by Lankester as thickened so as to form a knob, which projects at right angles to the line of the ligament.

On reference to Gegenbaur, it appears that he discovered this cartilage in the connective tissue which connected the innermost part of each entapophysis with a pyramidal projection of the integument which is situated at the base of each branchial appendage. Throughout he speaks of each cartilage as a 'Stückchen,' although of considerable thickness in diameter, 2''' thick. As far as I can understand his description, his pieces of cartilage were confined to the connective tissue close to the entapophyses, and corresponded to the knobs described by Lankester, and figured by Benham¹ in his paper. The extreme similarity in the appearance of the structure of this cartilage, as drawn in Lankester's picture, to that of the branchial cartilage of *Ammocetes*, and the similarity of its position, being, as it is, absolutely confined to the branchial region, and forming two longitudinal axial bands, together with the fact of its formation in a special kind of fibrous connective tissue, all pointed to the possibility of a correspondence between these entapophysial cartilaginous bands and the subchordal cartilaginous ligamentous bands of *Ammocetes*. Apparently, however, from Lankester's description, there were no branchial cartilaginous bars in *Limulus*, such as I expected to find if the entapophysial ligament corresponded to the subchordal bands

¹ *Trans. Zool. Soc.*, vol. xi.

of Ammiocoetes. I therefore determined to look for myself, and, through the kindness of Prof. Lankester, I was enabled to examine a well-preserved specimen of an adult *Limulus*. Imme-

FIG. 6.—Transverse sections through mesosoma of *Limulus* to show the anterior (A) and posterior (B) surfaces of a mesosomatic or branchial appendage. In each figure the branchial cartilaginous bar *Br.C* has been exposed by dissection on one side.

Ent, entapophysis; *Ent.l*, entapophysial ligament cut across; *Br.C*, branchial cartilaginous bar which springs from the entapophysis; *H*, heart; *P*, pericardium; *Al*, alimentary canal; *N*, nerve cord; *L.V.S*, longitudinal venous sinus; *Dv*, dorso-ventral muscle; *Vp*, veno-pericardial muscle.

diately I saw that a bar of cartilage of considerable size started from each entapophysis into each branchial appendage, so that by far the greatest and most conspicuous masses of this kind of

cartilage in *Limulus* were these branchial bars, and not the small masses in the entapophysial ligamentous bands. Wondering how Lankester could have missed such obvious structures, I turned to Benham's paper, written under Lankester's direction, and referred to in his paper, and there found these bars described and figured, but described not as *cartilage* but as *chitin*.

In fig. 6 I give drawings of the anterior and posterior aspects of one of the branchial appendages, in which it is seen that a conspicuous bar (*Br.C*) is marked out on the anterior chitinous surface of the basal part of the appendage by a difference of colour. This bar (*Br.C*) is apparently the chitinous bar described by Benham (*p* in his fig. 3, Pl. 74), to which various appendage muscles are attached, and is also, as far as I can understand Gegenbaur's description, the pyramidal projection at the base of the branchial appendage, which is connected with the entapophysis by means of the cartilaginous pieces. Upon cutting through the thin chitinous covering and removing the underlying muscles, we see, as is shown in fig. 6, that this bar is only covered with chitin, and that it is in reality a massive cartilaginous rod which extends across the whole base of the gill appendage, and springs from the cartilage at the entapophysis. The rods form, in fact, a regular series of branchial bars, which, like the corresponding branchial bars of *Ammocoetes*, are extra-branchial in position; for when the leaf-like branchial appendages are lying at rest, both the muscles of the appendage and the branchiæ may be spoken of as internal to this branchial bar. How it was possible for Lankester and Benham to miss this structure I cannot understand. This bar is composed of a firm homogeneous mass of cartilage surrounded by a distinct perichondrium, just as in the corresponding branchial bar of *Ammocoetes*; it is, in fact, very much more a true cartilaginous bar than the entapophysial ligament, which is largely composed of fibrous tissue with masses of cartilage in it, the cartilage formation being most extensive only at the region of the entapophyses, where the cartilage of the entapophysial ligament is continuous with that of the branchial bar, thus forming Lankester's 'knobs' and Gegenbaur's 'pieces.' In this respect, also, we see the similarity in the position of this cartilage with that of *Ammocoetes*; for, as already mentioned, the subchordal cartila-

ginous bands were especially thickened and conspicuous at the places where the branchial bars are given off. In fig. 5, A and B, I have attempted to represent the relative positions of the branchial skeleton of *Limulus* and *Ammocoetes* respectively.

Topographically, then, this cartilage corresponds most remarkably in the two animals, and gives very strong grounds for the belief that the branchial skeleton of the *Ammocoetes* arose from a branchial cartilaginous skeleton similar to that of *Limulus*. This conclusion is naturally immensely strengthened if the structure of the tissue is the same in both animals.

On the Structure of the Branchial Cartilages in Limulus.

What, then, is the structure of the cartilage in *Limulus*? Gegenbaur describes it as different from any other invertebrate cartilage, being composed of capsules, each of which contains a cell; it is surrounded by a connective-tissue perichondrium, and externally, at the perichondrial layer, the capsules are smaller, and ultimately form a homogeneous or at most fine granulated intercellular substance, which is directly continuous with the ground substance of the connective tissue.

Gegenbaur's description would correspond to a honeycomb of interstitial tissue surrounding separate cells, just as in the tissue of *Ammocoetes* or in parenchymatous vertebrate cartilage.

Lankester, however, says expressly that it resembles vertebrate cartilage in some respects, but differs in certain important characteristics. He states that capsules are formed as in cartilage, but the cells contain vacuoles which communicate with each other, so that this capsuligenous tissue forms a spongy or reticular cartilaginous lacunar system, and not a honeycomb system; it is therefore a modified part of the lacunar tissue, and not cartilage such as is found in vertebrates.

Lankester's picture of a section of this tissue is, to my mind, a good representation of the structure of the tissue, and it appears to me evident, from that picture alone, that his section is through a honeycomb kind of tissue, and not through a sponge. In all sections a clear wall of cartilage forming the capsule entirely surrounds each cell, just as in the corresponding sections of the branchial cartilage of *Ammocoetes*. The tissue can be described

in every way in precisely the same manner as the latter tissue. In both, vacuoles apparently appear between the cell and its capsule; in both, the explanation of such appearances is that we are dealing with a typical example of parenchymatous cartilage, in which, as is well known, although the cell may have originally filled the capsule, a shrinkage, or even a nearly total disappearance, of the cell-protoplasm is frequently observed in the contents of the older capsules, so giving the appearance of a small shrunk cell and a large vacuole surrounded by the wall of the capsule. It is perfectly true, as Lankester says, "there is nothing in this tissue corresponding to the general matrix of a hyaline cartilage. The capsules are all closely packed, without giving rise to any quantity of homogeneous inter-capsular substance."

Just so, the cartilage is of the embryonic or parenchymatous variety, and identical in its appearance with the branchial or soft cartilage of *Ammocoetes*; the description of Schaffer already quoted would apply to the description of this cartilage in *Limulus*. In one respect there is difference: the innermost axial layer of the branchial bar of *Limulus* is very apt to contain a specially hard substance, apparently chalky in nature, so that it breaks down on section, and gives the appearance of a broken down spongy mass; if, however, the tissue is placed in HCl solution first, it then cuts easily, and the whole tissue is seen to be of the same structure throughout, the main difference being that the capsular spaces in the axial region are much larger and much more empty of cell protoplasm than the smaller younger cells near the periphery.

The conclusion drawn from the histological appearance, that we have here a primitive cartilage of the same kind as the soft cartilage of *Ammocoetes*, is further confirmed and made certain by the similarity in the staining reactions of these two tissues. Just as in the soft cartilage of *Ammocoetes*, this tissue stains intensely purple with thionin, showing that it is a cartilage containing large quantities of chondro-mucoid, so also with picro-carminé, and better still with the double staining by hæmatoxylin and picric acid, this cartilage, like the *Ammocoetes* cartilage, takes on a red or deep bluish stain respectively, and does not stain yellow, as is the case with the cartilages of the trabeculæ and auditory capsule.

Very striking, as is seen in fig. 2, Pl. XIII., is the contrast between the cartilaginous branchial bar and the perichondrium surrounding it when the section has been stained with hæmatoxylin and picric acid, or with thionin. In the former case the fibrous perichondrium stains yellow, in contradistinction to the bluish colour of the cartilage; and in the latter, light blue, in contradistinction to the deep purple colour of the cartilage.

We may conclude from these staining reactions that this cartilage is composed mostly of a mucoid substance, while the fibres of the perichondrium surrounding it are more of the nature of ordinary white connective tissue, and contain a gelatinous rather than mucoid substratum. The chemistry of these substances will be considered later (p. 578).

On the Structure of the Muco-Cartilage in Limulus.

The observations of Gegenbaur and Lankester agree in the assertion that this cartilage is formed in connective tissue which is specially in connection with the entapophyses. Gegenbaur, in describing the different kinds of connective tissue found in *Limulus*, describes one particular kind as follows:—

“Connective tissue with almost homogeneous or slightly fibrillated intercellular substance, reminding one of a “Gallert Gewebe,” is the least common. It is found at the base of the gills in the neighbourhood of the inner projections of the chitinous skeleton (entapophyses), and in the neighbourhood of the stomach. The cells are star-like, their processes only slightly branched; on section they often appear as holes in the ground-substance.”

This tissue I imagine to be the fibrous tissue in which the cartilage of the entapophysial ligaments is formed.

Lankester looks upon it as a fibro-massive tissue, of the same kind as that which forms the substance of the entosternite.

Gegenbaur's description is more correct than that of Lankester: this tissue is not of the same character as that of the entosternite, and the difference is shown most markedly in the difference of reaction to staining reagents. The whole of this fibrous tissue in the neighbourhood of the entapophyses gives an intense purple reaction with thionin, while the fibrous tissue of the entosternite either gives no colour or stains a light blue colour, with the very faintest evidence of purple. In this purple

staining fibrous tissue of *Limulus* the cartilage is developed just as in the corresponding tissue of the *Ammocoetes*; and just as by its reaction with thionin it is possible to map out the position of the muco-cartilage in *Ammocoetes*, so by the same reaction it is possible to map out the position of the corresponding muco-cartilage in *Limulus*.

This tissue is clearly a connective tissue, containing a somewhat homogeneous mucoid ground-substance,—a tissue which, both in its staining reactions and its appearance, is comparable with the muco-cartilage of *Ammocoetes*.

In fig. 4, Pl. XIII., which is a section of the entapophysial ligament of *Limulus* stained with thionin, the formation of the parenchymatous cartilage in this muco-cartilage is shown; and in fig. 3, Pl. XIII., which is a section stained with thionin through the so-called pedicle, and the extra-hyal in an *Ammocoetes* before transformation, it is seen how the muco-cartilaginous bar of the extra-hyal is invaded by chondroblasts, and thus the commencement of the new cartilage is shown. Both these mucoid connective tissues in *Limulus* and in *Ammocoetes*, in which the parenchymatous cartilage is formed, may be called muco-cartilage; and we see that the entire disappearance of this tissue at the transformation of the lamprey is in accordance with my suggestion that the passage from *Ammocoetes* to *Petromyzon* is characterised by the casting off of invertebrate characteristics, and the putting on of a more complete vertebrate type.

On the Relation between the Internal Cartilaginous and External Chitinous Skeleton.

In the formation of muco-cartilage and consequent soft cartilage in *Limulus* we have a distinct clue to the formation of an internal skeleton in a group of animals like the Arthropoda, whose skeleton is external, and the question arises—How does *Limulus* form this muco-cartilage?

In the first place, it is distinctly formed in close connection with the entapophyses, that is, with ingrowths of the external chitinous covering; in the second place, the chitinous layer of the entapophyses, and indeed over the whole surface of the animal, is not of the same chemical structure throughout its

whole thickness. As Gegenbaur has pointed out, the chitinous layer is divisible into three layers—an internal, middle, and external layer; and he has described the differences in appearance between these layers. There is also a marked difference in staining reactions: thus the

Innermost layer stains, . . .	Thionin. Purple.	Picrocarmine. Red.
Middle layer stains, . . .	Blue.	Pink.
Outer layer stains, . . .	Not at all.	Yellow.

From this I conclude that the first formed soft layers of chitin show evidence of a body allied to the mucin group, while the later hard chitin is so altered as to give no evidence of such a reaction.

Further, I have examined carefully sections through the entapophyses, and the fibrous muco-cartilaginous tissue close against the entapophysis, and have failed to distinguish any layer of chitinogenous cells differing in character from the surrounding cells which distinctly form the fibrous tissue, which I have called muco-cartilage. My distinct impression at present is that this muco-cartilaginous tissue may be looked upon as formed of modified cells belonging to the chitinogenous layer, and that, therefore, the whole of the cartilage of the entapophysial ligament and of the branchial bars may be considered as a direct derivation from the external chitinogenous layer of cells. At the same time, considering the number of muscular attachments to the entapophyses and the difficulty of observing the chitinogenous cell layer when it is obscured by the invasion of the fibrous tissue of the muscular attachments, I do not feel certain as to the interpretation of my specimens, and do not desire to say more than that, in my opinion, there is a strong probability that this muco-cartilaginous tissue owes its character to its formation from altered chitinogenous cells, and that, therefore, whether the nests of cells which form cartilage in this tissue are chondroblasts which have come from without, or are modified cells of the muco-cartilage itself, the cartilage has arisen as a modification of chitin, a conclusion to which Gegenbaur was strongly inclined in 1858.

On the chemical side, the recent observations of Schmiedeberg¹

¹ *Archiv. f. exper. Pathol. u. Pharmac.*, Bd. 28, 1891.

on the constitution of cartilage point directly to the same conclusion, for he gives strong reasons for believing that cartilage possesses the same fundamental substance—viz., glykosamin—as chitin, and he concludes his observations in the following words:—

“ Thus, by means of glykosamin, the bridge is formed which connects together the chitin of the lower animals with the cartilage of the more highly organised creations.”

I come, then, to the conclusion that the cartilaginous internal branchial portion of the skeleton of Vertebrates arose, as in *Limulus*, from an external chitinous skeleton, by the alteration of chitinous ingrowths in connection with a series of branchial appendages. In this way the cartilaginous branchial bars and axial sub-chordal rods of *Ammocoetes* arose.

On the Origin of the Hard Cartilage of the Basi-cranial Skeleton of Ammocetes.

So far, I have discussed the origin only of one kind of cartilage found in *Ammocoetes*, viz., that which Parker called soft cartilage, in contradistinction to the cartilage of the auditory capsules and trabeculae, which he termed hard cartilage. The history of the vertebrate cartilaginous skeleton cannot be considered complete until the genesis of this hard cartilage, and especially of the basal trabeculae, has been explained, as well as the origin of the branchial cartilages.

We see that the structure of this hard cartilage of the trabeculae and auditory capsules resembles that of the soft, in so far that it consists of large cells with a comparatively small amount of inter-cellular substance. Schaffer, who has described it lately, considers that it is a nearer approach to hyaline cartilage than the soft, but yet cannot be called hyaline cartilage in the usual sense of the term. Its peculiarities and its differences from the soft are especially well seen by its staining reactions. Perhaps the most striking differences between the two kinds are to be found in their reactions to different dyes. I myself have been particularly struck with the effect of picrocarmine or combined hæmatoxylin and picric acid staining: in the case of the soft cartilage, the capsular substance stains respectively a brilliant red or blue,

while that of the hard cartilage is coloured a deep yellow, so that the junction between trabeculae and branchial cartilages is beautifully marked out. Then, again, with thionin, which gives so marked a reaction in the case of the soft cartilage, the hard cartilage of the auditory capsule is not stained at all, and in the trabeculae the deep purple colour is confined to the mucoid cement substance between the capsules, just as Schaffer has stated. (Cf. fig. 5, Pl. XIII., taken from Schaffer.) The same kind of reactions have been given by Schaffer: thus by double staining with hæmalum-eosin the hard cartilage stains red, the soft blue; and he points out that even with over-staining by hæmalum the auditory capsule remains colourless, just as I have noticed with thionin. He infers, precisely as I have done from the thionin reaction, that chondro-mucoid, which is so marked a constituent of the soft cartilage and of the muco-cartilage, is absent, or present in slight quantities, in the hard cartilage. Similarly, he points out that double staining with tropæolin-methylviolet stains the hard cartilage a bright orange colour, and the soft cartilage a violet.

The evidence, then, shows clearly that a marked chemical difference exists between these two cartilages, which may be expressed by saying that the one contains very largely a basophil substance, which we may speak of as belonging to the class of chondro-mucoid, while the other contains mainly an oxyphil substance, probably a chondro-gelatine substance.

We may perhaps go further, and attribute this difference of composition to a difference of origin; for we see that, whereas the soft cartilage is invariably formed in a special tissue, the muco-cartilage, which shows by its reaction how largely it is composed of a mucoid substance, the hard cartilage is certainly in the case of the cartilage of the cranium, where its origin has been clearly made out, formed in the membranous tissue of the cranium of *Ammocoetes*—i.e., in a tissue which stains light blue with thionin, and contains in all probability a gelatinous rather than a mucoid substratum.

The best opportunity of finding out the mode of origin of the hard cartilage is afforded at the time of transformation, when so much of this kind of cartilage is formed anew. Unfortunately, it is very difficult to obtain the early transformation

stages, consequently we cannot be said to possess any really exhaustive and definite account of how the new cartilages are formed. Bujor,¹ Kaensche,² and Schaffer³ all profess to give a more or less definite account of their formation, and the one striking impression left on the mind of the reader is how they vary.

In one point only are they agreed, and in that I also agree with them, viz., the manner in which the new cranial walls are formed. Schaffer describes the process as the invasion of chondroblasts into the homogeneous fibrous tissue of the cranial walls. Such chondroblasts not only form the cartilaginous framework, but also assimilate the fibrous tissue which they invade, so that finally all that remains of the original fibrous matrix in which the cartilage was formed are these lines of cement substance between the groups of cartilage cells which, containing some basophil material, are marked out, as shown in fig. 5, Pl. XIII.

We may therefore conclude, from the investigation of *Ammocoetes*, that the basi-cranial skeleton arose as two trabecular bars, to which muscles were attached, situated bilaterally with respect to the central nervous system. These bars were composed of tendinous material, with a gelatinous rather than a mucoid substratum, in which nests of cartilage-cells were formed, the cartilaginous material formed by these cells being of the hard variety, not staining with thionin, and staining yellow with picrocarmine, etc. By the increase of such nests and the assimilation of the intermediate fibrous material, the original fibrocartilage was converted into the close-set semi-hyaline cartilage of the trabeculæ and auditory capsules, in which the fibrous material still marks out by its staining reaction the limits of the cell clusters.

Such I gather to be Schaffer's conclusions, and they are certainly borne out by my own and Miss Alcock's observations. As far as we have had an opportunity of observing at present, the first process at transformation appears to consist of the invasion

¹ *Revue biologique du Nord de la France*, vol. iii., 1891.

² *Schneider's Beiträge*, vol. ii. p. 219, 1890.

³ *Op. cit.*

of the fibrous tissue of the cranial wall by groups of cells which form nests of cells between the fibrous strands. These nests of cells form round themselves capsular material, and thus form cell territories of cartilage, which squeeze out and assimilate the surrounding fibrous tissue, until at last all that remains of the original fibrous matrix are the lines of cement substance which mark out the limits of the various cell groups.

At present I am inclined to think that both soft and hard cartilage originate in a very similar manner, viz., by the formation of capsular material around the invading chondroblasts, and that the difference in the resulting cartilage is mainly due to the difference in chemical composition of the matrix of the connective tissue which is invaded. Thus the difference may be formulated as follows:—

The hard cartilage is formed by the invasion of chondroblasts into a fibrous tissue, which contains a gelatinous rather than a mucoid substratum, in contradistinction to the soft cartilage which is formed probably also by the invasion of chondroblasts, in a tissue, the muco-cartilage, which contains a specially mucoid substratum.

On the Hard Cartilage of Limulus.

The origin, then, of the basi-cranial cartilaginous framework of *Ammocoetes* resolves itself into this question—Is there any peculiar tissue of a cartilaginous nature in *Limulus* and its allies, situated in the prosomatic region, which is entirely separate from the branchial cartilaginous skeleton, which acts as a supporting internal framework, and contains a gelatinous rather than a mucoid substratum?

It is a striking fact, common to the whole of the group of animals to which our inquiries, deduced from the consideration of the structure of *Ammocoetes*, have in every case led us in our search for the vertebrate ancestor, that they do possess a remarkable internal semi-cartilaginous skeleton in the prosomatic region, which gives support to a large number of the muscles of that region, which is entirely independent of the branchial skeleton, and markedly differs in its chemical reactions

from that cartilage, in that it contains a gelatinous rather than a mucoid substratum.

This striking internal prosomatic skeleton is known by the name of the entosternite or plastron; and, except in *Limulus*, the scorpions, and whole arachnid group, is found, significantly enough, only in *Apus*.

The meaning of the entosternite has been discussed by Schimkéwitsch,¹ especially in connection with the entosternite of the Thelyphonidæ, based partly on his own observations, partly on those of Tarnani.² I myself have examined this organ in *Hypoctonus formosus*, and in young and old specimens of *Thelyphonus caudatus*.

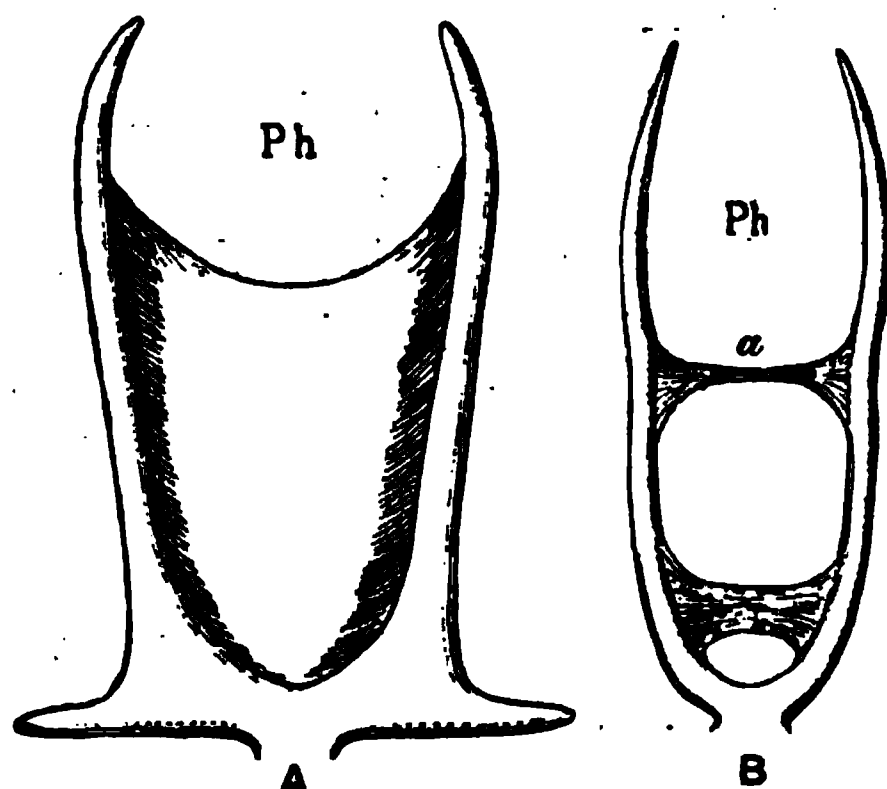


FIG. 7.—A, Entosternite of *Limulus*; B, Entosternite of *Thelyphonus*; Ph, Position of pharynx.

Very different is the entosternite of the Thelyphonidæ from that of *Limulus* or the scorpions: whereas the latter consists of a massive plate which lies between the infra-oesophageal ganglia and the gut (fig. 7, A), the former consists, as Schimkéwitsch describes it, of two lateral trabeculæ, crossed by three transverse trabeculæ, so that the appearance of the entosternite of *Thelyphonus* is represented in the fig. 7, B, in contradistinction to that of *Limulus*, fig. 7, A. The entosternites of *Hypoctonus formosus* and

¹ "Sur la structure et sur la signification de l'Endosternite des Arachnides," *Zool. Anzeig.*, 1893, p. 300.

² *Revue des Sciences Naturelles, Petersbourg*, 1890, p. 215.

Thelyphonus caudatus closely resemble this figure, and in all we see that the transverse trabecula *a*, which is nearest to the place where the œsophagus passes out of the conjoined mass of the supra- and infra-œsophageal ganglia, is very thin; that then there is a long space below which the infra-œsophageal ganglia is lying, before the next transverse trabecula is reached, so that the greater portion of the entosternite is formed of two lateral trabeculæ, the transverse trabeculæ being mostly at the posterior part.

Naturally, no part of the entosternite lies between the infra-œsophageal ganglia and all that part of the intestine which is completely enclosed by the nervous system, and indeed the first transverse trabecula which roofs the nervous system is found some little distance beyond the termination of the supra-œsophageal ganglion mass. The anterior horns, then, of the trabeculæ lie laterally and slightly ventral to the central nervous system, and are called by Lankester and Benham the sub-neural portion of the entosternite; and it is easy to see that, with a more extensive growth of the nervous material dorsally, such lateral horns might be caused to take a still more ventral position. Judging, then, from the entosternite of *Thelyphonus*, it is not difficult to suppose that a continuation of the same growth of the brain region of the central nervous system would cause the entosternite to be separated into two lateral trabeculæ, which would then take up the ventro-lateral position of the two trabeculæ of *Ammocoetes*.

On the other hand, it might be that two lateral trabeculæ, similar to those of *Thelyphonus*, and situated on each side of the central nervous system, were the original form from which, by the addition of transverse fibres running between the gut and nervous system, the entosternite of *Thelyphonus* and of the scorpions, etc., were formed. From an extensive consideration of the entosternite in different animals, Schimkéwitsch has come to the conclusion that this latter explanation is the true one. He points out that the lateral trabeculæ can be distinguished from the transverse by their structure being much more cellular, less fibrous, and the cell cavities more rounded, or, as I should express it, the two lateral trabeculæ are more cartilaginous, while the transverse are more fibrous. Schimkéwitsch, from observations of structure and from embryological investigations, comes to the

conclusion that the entosternite was originally composed of two parts:—

1. A transverse muscle corresponding to the adductor muscle of the shell of certain crustaceans, such as *Nebalia*.

2. A pair of longitudinal mesodermic tendons, which may have originally been formed out of a number of segmentally arranged mesodermic tendons, and are crossed by the fibrils of the transverse muscular bundles.

These paired tendons of the entosternite he considers to correspond to the intermuscular tendons, situated lengthways, which are found in the ventral longitudinal muscles of most arthropods.

It is clear from these observations of Schimkéwitsch that the essential part of the entosternite consists of two lateral trabeculæ, which were originally tendinous in nature, and have become of the nature of cartilaginous tissue by the increase of cellular elements in the matrix of the tissue: these two trabeculæ function as supports for the attachment of muscles, which are especially attached at certain places. At these places transverse fibres belonging to some of the muscular attachments cross between the two longitudinal trabeculæ, and so form the transverse trabeculæ.

In this tissue, according to the observations of Ray Lankester, we see cartilage beginning to form. In his paper he gives pictures of the structure of the entosternite, showing its resemblance to a fibro-cartilage. The striking characteristics are the nests of cells in between the fibrous tissue. Lankester does not differentiate the different parts of this tissue by any micro-chemical staining reactions, but simply says that Schäfer examined it chemically for him, and found in it mucin, and on purely negative evidence, chitin; he also says that it does not contain gelatine or chondrin. In a foot-note Schäfer is more cautious, and explains that the only positive result of his examination was the presence of mucin.

In order to make up my mind as to the nature of the entosternite, I tried, in the first instance, the action of thionin, and found, in striking contrast to the branchial cartilages or the muco-cartilage, that it took no purple stain, but only a pale blue tint, with the very slightest tinge of purple. The same reac-

tion was seen with the entosternite of *Thelyphonus* as with that of *Limulus*, and in both cases the appearance closely resembled that seen in sections of ordinary tendon of any of the higher vertebrates. Gelatinous tissues give a great contrast to mucoid tissues in their staining reaction with thionin, and lead distinctly to the conclusion that cartilages, the matrix of which stains only a light blue colour with thionin, in which, therefore, there is no real staining reaction, possess a gelatinous rather than a mucoid substratum. So clear was the contrast between the thionin staining of the branchial cartilages and the entosternite cartilage that I felt sure a similar reaction would be manifested by picrocarmine, or by hæmatoxylin and picric acid.

Most striking is the effect of staining the entosternite of *Hypoctonus* with hæmatoxylin and picric acid. In this tissue, especially, as already mentioned, in the two lateral trabeculæ, nests of cartilage cells are found, as is seen in fig. 6, Pl. XIII. Each of these cells forms around itself a mass of translucent colloid-looking material, which stains intensely yellow with the picric acid, while the fibres between these cell nests stain a blue-brown colour, partly from hæmatoxylin, partly from the picric acid. Where these nests are thickly congregated the fibrous material between them is thinned down to mere threads, as is seen in the figure. Here and there single cells surrounded by the same substance are seen.

A similar appearance is described in *Mygale* by Ray Lankester, and there it is interesting to note that these peculiar cell nests, with their colloid material, are confined, according to him, to the lateral portions of the entosternite. So also we see in the entosternite of *Limulus*, of *Scorpio*, etc., that the original lateral trabeculæ are conspicuous as two lateral thickened bars in its fibrous tissue.

I conclude, therefore, from the whole evidence, that the entosternite of *Limulus*, etc. arose as two trabecular bars, to which muscles were attached, situated bilaterally with respect to the central nervous system. These bars formed two mesodermic longitudinal tendons, composed probably of a number of tendons originally arranged metamerically, with a gelatinous rather than a mucoid substratum, in which nests of cartilage cells were

formed, the cartilaginous material formed by these cells being of the hard variety, not staining with thionin, and staining yellow with picrocarmine, etc.

Further, a marked contrast exists between these two cartilaginous structures with respect to their chemical analysis.

Owing to the kindness of Dr F. Lee of Columbia College, I had at my disposal a considerable number of living examples of *Limulus Polyphemus*. Gegenbaur's investigations into the chemical nature of the *Limulus* cartilage, and also, I imagine, Schäfer's investigation into the chemistry of the entosternite, were made on alcohol specimens, so that the solubility of the tissues in various reagents was almost certainly different from their solubility in the fresh condition. I have made use of the tissues absolutely fresh, taken out of the living animal; and in a large *Limulus* the entosternite on the one hand, and the mass of the branchial cartilages on the other, give a very sufficient amount of material for analysis. This material was put into the hands of Mr Eichholtz, and the following is his report on the constitution of these two tissues.

Experiments with the Entosternite.

1. The entosternite was carefully scraped and washed free from muscle and glandular matter, and cut into thin strips. The finely divided material was thymolised and immersed in baryta water for four days to extract any mucin if possible. After this time the liquid was poured off and filtered, and tested with dilute acetic acid. It was impossible to discover anything more than the merest traces of any precipitation, indicating that mucin, if present, is present only as a trace.

The solution treated with a dilute thionin solution (which changes from violet blue to purple pink in presence of mucin) equally indicated the absence of mucin.

2. In a second experiment the entosternite was again cleansed and finely divided. It was now boiled for one hour under a condenser with distilled water, when *most of it* went into solution, a small amount of insoluble residue remaining behind. The solution was filtered off, and gave the following clear indications of the presence of gelatine :—

- (a) It precipitated with corrosive sublimate solution.
- (b) It precipitated with tannic acid.
- (c) It gave *no* reaction with Millon's reagent.
- (d) There was a very faint, almost imperceptible xanthoproteic reaction.

(c) There was no biuret reaction.

So that the water and baryta extracts lead one to the conclusion that the Entosternite belongs to the connective tissues; and from the small traces of mucin found, compared with the large amount of gelatine, one is inclined to classify it with the white fibrous connective tissues.

Experiment with the Branchial Cartilage.

The pieces of branchial cartilage were cleansed from adherent tissue, washed, and divided into small pieces. The material was then immersed in baryta water, a few drops of thymol added, and left for four days. The liquid was now poured off and filtered. On careful addition of acetic acid, a copious white precipitate was formed, soluble in alkali. The liquid reacted characteristically with dilute thionin solution, changing from violet to bright purplish pink. These two reactions together point conclusively to the presence of mucin.

The residue insoluble in baryta was washed from baryta, and boiled for half an hour in water under a condenser, when it mostly dissolved, leaving a slight powdery white residue. On cooling, a jelly-like film formed on the sides of the flask, indicating that *gelatin* had been dissolved by the boiling. The presence of a material in these bodies yielding both mucin and gelatin points conclusively to its *cartilaginous nature*.

In either case the chemical record agrees with the physical properties of the tissue, for the entosternite is a tough membranous plate, and the branchial cartilages are much more rigid and friable in nature.

It is perfectly clear from this report by Eichholtz that the main substance in the branchial cartilages is of a mucoid nature, to which a small amount of a gelatinous substance must be added: doubtless, some of this gelatinous film observed must be attributed to the fibrous perichondrial layer which surrounds each cartilaginous bar.

Equally clear is it that the main substance in the entosternite is of a gelatinous nature, and that mucin is present only as a trace,—exactly the reverse of Lankester's statement. In both cases there is some insoluble residue, but there is at present not sufficient evidence to say whether such residue contains chitin. Most certainly it is impossible to say that the entosternite is composed of chitin and mucin, as Lankester does: it is a markedly gelatinous tissue, like vertebrate tendon, containing a trace of mucin, and that is all that can be said at present.

We see, then, in *Limulus* and the scorpion groups the com-

mencement of the formation of an internal skeleton in two directions:—

1. The formation of soft cartilage in a special mucoid tissue—muco-cartilage, derived apparently from the modification of chitin forming cells.

2. The formation of hard cartilage in collagenous tissue, which formed originally the tendons of muscles.

Further, it is a striking fact that these two kinds of cartilage form respectively (1) a branchial skeleton, which is confined to the mesosomatic region; (2) the supporting skeleton of the entosternite, which is confined to the prosomatic region.

Such, then, appears to me to be the reason why the branchial or mesosomatic skeleton of *Ammocoetes* is formed of soft cartilage, while the basi-cranial or prosomatic trabeculæ are formed of hard cartilage; why these two primitive skeletal parts are formed independently of each other, because they are the direct descendants of the branchial and entosternite cartilaginous skeletons of the invertebrate ancestor of the *Ammocoetes*. I will not here discuss the question whether the auditory capsules and the parachordals arose separately from the trabeculæ, but will leave the consideration of that question to the chapter on the origin of the auditory apparatus. The study of the cartilaginous structures of the *Ammocoetes*, in the light of my working hypothesis, has led to a perfectly harmonious and simple explanation of the way in which the external skeleton of the invertebrate became converted into the internal skeleton of the vertebrate, and gives us another fixed point from which to make further comparisons between the head region of the two groups of animals, such as will be elucidated in the forthcoming chapters. The further evolution of the vertebrate skeleton, as seen in the formation of the various cartilaginous structures at transformation, I will leave to a subsequent paper; for although I have examined the transforming animal, for this express purpose, for some years past, I have not been able to obtain a sufficient series of the stages of transformation to enable me to make up my mind on the nature of the steps by which the new cartilage is formed in all cases.

Such, then, in accordance with my hypothesis, is the manner in which the vertebrate skeleton arose. We see further that such origin is in agreement with the six principles laid down; for—



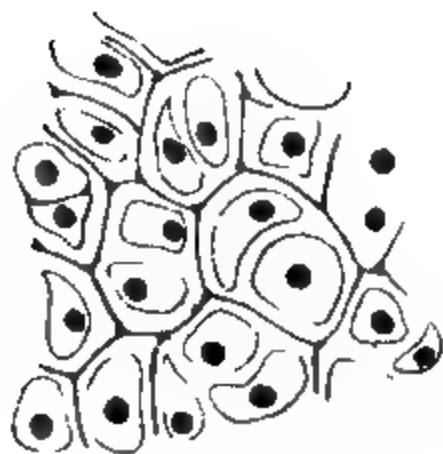
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6

1 and 2. The variations by which the internal cartilaginous skeleton is formed in the group of *Limulus* and the scorpions is in absolute accord with the method of formation in *Ammocoetes*.

3. The function of this primitive vertebrate skeleton is a direct continuation of its function in the invertebrate ancestor.

4. The muco-cartilage, which from its disappearance at transformation and its absence in the higher vertebrates may be classed among the rudimentary tissues, is found as a most important constituent in *Limulus*.

6. Here also embryology shows us most clearly how that skeleton arises, and, as explained, is in absolute accord with my hypothesis. One difficulty only exists of the same character as already explained in Part I., dealing with the central nervous system, viz., that the cartilaginous vertebrate skeleton is derived from mesoblast, while the chitinous ingrowths and their modifications, from which, apparently, the branchial skeleton of *Limulus* arises, must be looked upon as epiblastic formations. Although I consider the germ layer theory to be at the present time in a state of chaos, and therefore that it is not advisable to lay any great stress on arguments derived from the origin of a tissue from this or that layer, yet it is worth while pointing out that Kuppfer, in his most recent paper, asserts most definitely that the branchial cartilages in *Ammocoetes* are not mesoblastic, but are epiblastic in origin.

DESCRIPTION OF PLATE XIII.

Fig. 1. Portion of branchial cartilage of *Ammocoetes*, with its perichondrium; stained with thionin.

Fig. 2. Portion of branchial cartilage of *Limulus*, with its perichondrium; stained with thionin.

Fig. 3. Muco-cartilage of *Ammocoetes*, with cartilage of extra-hyal forming in it; stained with thionin.

Fig. 4. Muco-cartilage of entapophysial ligament of *Limulus*, with cartilage forming in it; stained with thionin.

Fig. 5. Cartilage of trabeculae of *Ammocoetes* (after Schaffer, *loc. cit.*, Taf. xxvii. fig. 7); stained with hæmatoxylin and picric acid.

Fig. 6. Nests of cartilage cells in entosternite of *Hypoctonus*; stained with hæmatoxylin and picric acid.

THE GENITO-URINARY ORGANS OF THE FEMALE
INDIAN ELEPHANT.¹ By A. M. PATERSON, M.D.,
Professor of Anatomy, University College, Liverpool; and
R. C. DUN, M.B., *Demonstrator.* (PLATES XIV., XV.)

THE elephant which forms the subject of this memoir was poisoned by aconitine at Aintree, near Liverpool, on May 8th, 1897. For the body we are indebted to Mr Cross, of Liverpool, from whose menagerie the animal had escaped in a state of frenzy. She weighed 3 ton 12 cwt., and measured over 9 feet at the shoulder. Although stated to be twenty years old, the condition of the skeleton shows that she had not attained her full growth.

I. URINARY ORGANS.

1. THE KIDNEYS are of equal size, and are generally oval in form, measuring 15 ins. in length and $10\frac{1}{2}$ ins. in breadth. The left kidney weighs $6\frac{3}{4}$, the right $5\frac{3}{4}$ lbs. Each presents a smooth, rounded dorsal surface, and a lobulated ventral surface, with the hilum situated about its middle. The mesial border of the left kidney (fig. 12) has two notches upon it, continued into clefts which extend to the hilum. The mesial border of the right kidney shows three notches which reach the hilum. The lateral border of the left kidney presents no indentation, but in the right a slight notch is found towards the lower part. *The hilum* (fig. 12) is situated upon the ventral surface, forming a large shallow space with an irregular margin, due to the projection of the surrounding lobules. It contains the branches of the ureter, renal artery, and vein. *The lobules* are present only upon the ventral surface. They are imperfectly separated by notches upon the borders of the kidneys, and round the margins of the hilum, and by clefts traversing the ventral surface. The left kidney presents six lobes (fig. 12), which are named from their

¹ Read at the meeting of the Anatomical Society, Feb. 2, 1896.

position—superior (1), anterior superior (2), anterior inferior (3), inferior (4 and 5), posterior inferior (6), posterior superior (7).

The right kidney has seven lobes—superior (1), anterior (2), anterior inferior (3), inferior (4), posterior inferior (5), postero-medial (6), posterior superior (7).

The inferior and posterior inferior lobes of the right kidney are indistinctly separated from each other by a notch at the margin of the hilum, and together represent the inferior lobe (4 and 5) of the left side. The papillæ opening into the calices numbered twenty-three on the right side and twenty-seven on the left. The number in relation to the individual lobes varies from two to six.

VESSELS AT THE HILUM.—*The left renal artery* (fig. 12, Art.) divides into two main parts, anterior and posterior. From these, numerous smaller branches are irregularly distributed to the various lobes. *The right artery* at the hilum gives off three main branches, which are further subdivided into smaller branches distributed to the lobes. The arterial branches at the hilum first occupy a position external to the branches of the ureter and veins, but are subsequently placed between the veins externally and the ureters internally. In the interval between the inferior and posterior inferior lobes of the right kidney, a small artery, whose source was not ascertained, pierces the ventral surface of the kidney midway between the circumference and the hilum. *The renal veins* (fig. 12, V.) in their general arrangement correspond with the arteries, several branches passing from each lobe. They emerge nearer the centre of the hilum than the arteries and ureters, but as the larger branches are formed, they lie outside these structures.

2. THE URETERS.—*The left ureter* (fig. 12, Ur.) is formed at the hilum by two main branches, superior and inferior. The superior division receives three smaller branches connected with the superior anterior superior and posterior superior lobes. The inferior division is also formed by three branches coming from the anterior inferior, posterior inferior, and inferior lobes. *The right ureter* is similarly formed by the union of superior and inferior branches. The superior branch is connected with the anterior superior, superior,

posterior superior, and postero-median lobes; the inferior branch with the anterior inferior, inferior, and posterior inferior lobes. The relations of the branches of the ureter to the other structures at the hilum are similar on both sides. As they emerge from the hilum they occupy a position intermediate between the arteries and veins, but as the larger branches are formed, they lie mesial to both these structures.

The ureters begin opposite the site of the ovary, at the base of the broad ligament, and extend along the line of its attachment (fig. 7, Ur.). They pass on either side of the rectum and uterus, and end at the side of the base of the bladder, separated from each other by a distance of $4\frac{1}{2}$ inches. The ureters are accompanied in their course by branches of the renal and internal iliac arteries, and are crossed by the obliterated hypogastric artery. The diameter of each is $\frac{3}{8}$ inch. The right ureter measures 2 feet 3 inches; the left 2 feet.

3. BLADDER AND URETHRA.—The bladder (figs. 1, 2, 3, 5, Bl.), when moderately distended, is oval in form, with its long axis directed backwards and downwards. Its greatest length is 12 inches; its greatest width laterally and antero-posteriorly 7 inches. It is partially covered by peritoneum, reflected on its back and side from the uterus and broad ligament. The peritoneum clothes the dorsum and sides of the bladder in its anterior half, and is reflected from it on the pelvic and abdominal walls. At the sides of the bladder, in the angle of reflexion on the pelvic wall, it is raised up into a thick rounded fold by the obliterated hypogastric artery and branches of the internal iliac arteries beneath. In connexion with each of these ridges, a secondary fold of peritoneum, free from contents, is prolonged upwards alongside the bladder. Below and behind, the bladder is further covered by a thick dense layer of pelvic fascia, which intervenes between it and the uterus. The two ureters open into the wall of the bladder, posteriorly and superiorly, $4\frac{1}{2}$ inches from one another, and 9 inches from the neck of the bladder (figs. 1, 2, 3, Ur.). They pierce the wall of the bladder obliquely, and open on the interior of the organ at different levels, the right ureter being 7 inches from the neck, the left ureter 9 inches. The openings are 3 inches apart. Each opening is valvular, with a sharp concave upper edge, the

border of a thin translucent reduplication of the mucous membrane, 2 inches long on the right side, 1 inch in length on the left side (fig. 5, Ur.). The difference in position of the internal openings is due to the shorter course of the left ureter through the bladder wall.

The muscular wall of the bladder (fig. 1) is thick and strong, consisting of a thick layer of pale muscular fibres, interlaced together in all directions over the surface of the organ. Under the muscular coat is a loose layer of submucous tissue, covering the smooth mucous membrane. The mucous membrane is raised into a thin ridge (fig. 5) in the middle line at the neck of the bladder, which disappears when it is put on the stretch.

The neck of the bladder (urethra) is short and thick, 2 inches in length, and lies over the terminal part of the vagina. The upper half is different in structure from the lower half. The upper half is surrounded by a ring of muscular fibres, forming a distinct sphincter (figs. 1 and 5, Sph. V.) continuous behind with the muscular wall of the bladder, but clearly demarcated from it: continuous in front with the bulbo-cavernosus muscle. Beneath the sphincter is a loose, thin mucous membrane, joined behind by the slight ridge occupying the floor of the bladder. The lower half is invested by the fibres of the bulbo-cavernosus muscle (fig. 1); beneath this is placed a ring of submucous tissue, to which the smooth mucous membrane is adherent (figs. 3, 5, Ure.).

The posterior opening into the bladder is smooth, and passes directly into the bladder wall. The anterior opening into the urogenital canal is a rounded thick-lipped aperture, $\frac{3}{4}$ inch in diameter, placed above the vaginal opening (fig. 4, Ure.).

II. GENERATIVE ORGANS.

The generative organs are naturally separated into two series: (1) those enclosed in the layers of the broad ligament, and contained in the abdominal and pelvic cavities, and (2) those outside the peritoneum and in the perinæum.

THE BROAD LIGAMENT AND ITS CONTENTS.—(a) The broad ligament (figs. 6 and 7) is a membranous fold of peritoneum attached to the dorsal wall of the abdominal and pelvic cavities. It fades away anteriorly in relation to the diaphragm, to which it

is attached by a diaphragmatic ligament (D.L.); in the pelvic cavity it forms a simple continuous partition between the rectum and the bladder, its two layers being reflected upwards on the rectum behind, and downwards on the bladder in front.

Its dimensions are not the same on the two sides. On the right side its free edge measures 28 inches in length; on the left $37\frac{1}{2}$ inches. Its depth is 17 inches on the right side, 16 inches on the left, alongside the uterus at the side of the middle line. Its depth is 13 inches in the middle of its extent; and at the hilum of the ovary, $5\frac{1}{2}$ inches on the right and 3 inches on the left side. It forms a convex pendulous fold, with a thickened rounded free border, which contains the Fallopian tube (fig. 7, F.T.). The Ureter (Ur.) runs backwards along its attached margin. The first part of the uterus (Co. Ut.) is placed between its two layers in the middle line; and the ovary (Ov.) and opening of the Fallopian tube occupy the inner aspect of the ligament near its diaphragmatic attachment. It also encloses layers of muscle, along with vessels and nerves. Near the uterus the lower half of the ligament is thickened, apparently on account of the presence of an increased amount of muscular tissue. A secondary fold of peritoneum exists on the inner side of each broad ligament (fig. 6, Sec.) opposite to and below the attachment of the ovary. This is much larger and more complex on the right, its attachment measuring 20 inches; and it is roughly triangular in form, with an irregular margin, provided with long and narrow as well as flat and rounded projections and subordinate folds. On the left side the fold is simpler, smaller, and roughly quadrilateral. It measures 9 by 7 inches.

Muscular Tissue of the Broad Ligament.—Beneath the peritoneum the broad ligament is provided with two loose sheets of muscular fibres which radiate outwards from the middle line (fig. 7, M.M.). They form thick layers on the front and back of the uterus, thinning out on each side in relation to the broad ligament, where they are separated by the vessels and nerves. They become more abundant again at the edge of the broad ligament, and form a loose tubular investment for the Fallopian tube. Both Fallopian tubes and uterus lie almost free in this loose investment of muscle; the muscular fibres, indeed, only require to be cut through in order to expose the tubes. Between the

two horns of the uterus the muscular strata form a thick continuous layer, over which the peritoneum is reflected, so as to give to the broad ligament a simple continuous margin in the middle line. The strata of muscle pass downwards over the front and back of the uterus, so as to form an investment for its extra-peritoneal portion; when traced forwards the muscular tissue passes beneath the ovarian sac, and entering the ovario-fallopian and diaphragmatic ligaments, finally loses itself on the diaphragm.

Contents of the Broad Ligament.

THE OVARY

(Ov., figs. 6, 7, 11) is placed near the anterior end of the broad ligament on its mesial aspect. It occupies *the ovarian pouch* (S.), a shallow concavity, which measures 3 inches from before backwards, and $2\frac{3}{4}$ inches from above downwards. The pouch is bounded dorsally by the ovarian hilum, ventrally by a fold of peritoneum which is continuous with the broad ligament. The ventral half of the margin of the pouch is formed by the thin irregular edge of the *infundibulum* (I.). The pouch is divided into two parts: a dorsal portion, smooth, pale and glistening, and circular, which contains the ovary; and a ventral half (infundibulum), larger in size, crescentic in shape, dull and of a dark red colour, and marked by parallel folds, leading to the commencement of the Fallopian tube.

Attachment of the Ovary.—The ovary is attached by its hilum (fig. 11, Hi.) to the dorsal border of the ovarian pouch, and hangs downwards. The vessels enter the substance of the ovary at this spot; and at the attachment of the ovary there is a considerable increase in the thickness and toughness of the tissue beneath the peritoneum of the broad ligament.

The Ovarian Ligaments are two in number. The *diaphragmatic* ligament (D.L.) passes forwards from the ovarian hilum to the diaphragm, where it fades away. It is 9 inches in length, thick and fibrous, and invested by a dense layer of muscular fibres covered by peritoneum. The *ovario-fallopian* ligament (O.F.L.) passes backwards from the hilum of the ovary to

the Fallopian tube. It is composed almost entirely of muscular fibres, continuous with the investment of the Fallopian tube.

The left ovary measures in its greatest (antero-posterior) diameter $2\frac{3}{4}$ inches. The line of attachment at the hilum is $1\frac{1}{4}$ inches; the length from hilum to margin is $1\frac{1}{2}$ inches; and its thickness is 1 inch. It is firm and reddish-grey in colour, and is covered by a glistening investment of peritoneum. The ovary is marked on its surface by numerous shallow sulci, separating it into lobules; on its free lower border three wider sulci are present, crossing it obliquely, and separating off four lobules. To the most anterior of these lobules was attached a small pendulous cyst, measuring, with its peduncle, 1 inch in length. It is noteworthy that the *right ovary*, which measures $2 \times 2\frac{1}{4}$ inches, when removed from the body, was soft and pulpy, divested of peritoneum, and covered by shreds of soft white material (lymph) which could be easily stripped from its surface. Its surface was wrinkled and corrugated; and along its free border ran a fissure, which partially separated the organ into halves. The condition of the right ovary may have been the cause of the furious outbreak which led to the escape of the elephant from Mr Cross's menagerie.

Ovarian Vessels.—The *ovarian artery* (O.A., figs. 7, 11) is a branch of the renal artery, and passes outwards directly over the ventral surface of the kidney to reach the ovary. It supplies branches to the ovary and ovarian pouch, and extending along the ovario-fallopian ligament, can be traced for a considerable distance in the broad ligament. The ovarian vein is of great size. It is formed near the hilum of the ovary by the union of several large veins from the ovary and broad ligament. Its exact termination was not found. Its end was cut near the renal vein.

Parovarium. (Par., fig. 7) (?). A plexiform mass of tubules, occupying an area of $1\frac{1}{2}$ inches, was placed in the fold of peritoneum separating the ovarian pouch from the infundibulum. No distinct duct could be found. The mass was connected with the muscular investment of the Fallopian tube by a tough fibrous band running along the ovario-fallopian ligament.

THE FALLOPIAN TUBE.

The Fallopian tube (fig. 7, F.T.) extends from the infundibulum through the broad ligament to the middle line, where it unites with its fellow of the opposite side to form the body of the uterus.

The Infundibulum (I.) is a large crescentic pouch 5×5 inches in extent, forming the lower (ventral) half of the ovarian pouch. Its anterior angle is attached to the hilum of the ovary; its posterior angle is joined to the margin of the ovarian pouch. The anterior portion of the pouch is connected to the diaphragm and ovario-diaphragmatic ligament by a fold of peritoneum, thickened by a mass of muscular fibres prolonged forward from the lining of the ovarian pouch. Posteriorly, the pouch is connected to the broad ligament by a peritoneal fold (the wall of the ovarian pouch), greatly thickened by the presence between its layers of the (?) parovarium. The interior of the sac is marked by a large number of folds or rugæ, which converge from minute fimbriæ on the edge of the sac to the orifice of the Fallopian tube. The rugæ are small, and irregular in size and arrangement. Many of them end short of the border of the sac in minute fimbriæ.

The orifice of the Fallopian tube (*ostium abdominale*) figs 6, 7, 11, Ost.) is placed about the middle of the back of the sac. It is a slit-like opening, $\frac{1}{2}$ inch in diameter on the right side, $\frac{3}{4}$ inch on the left side. On its mesial side is a prominent lip—a thickening marked by grooves and ridges. Externally the orifice is continuous with the interior of the sac of the infundibulum, and is scored by the converging rugæ.

The Fallopian tube forms a simple narrow tube, which curves behind the ovarian sac, along the ovario-fallopian ligament, and between the layers of the broad ligament. Its length is 51 inches on the right, 57 inches on the left side, and its calibre varies from $\frac{1}{4}$ to $\frac{1}{2}$ inch. It may be divided into four portions—(1) a funnel-shaped mouth, (2) a portion in the wall of the ovarian sac, (3) a part in relation to the ovario-fallopian ligament, and (4) a part in the broad ligament.

The dimensions (in inches) of the different parts are as follows:—

	Width.		Length.	
	R.	L.	R.	L.
Funnel-shaped mouth,	$\frac{1}{2}$ "	$\frac{3}{4}$ "	1	1
Part behind ovarian sac,	$\frac{1}{8}$ "	$\frac{1}{8}$ "	6	8
Part in relation to ovario-fallopian ligament,	$\frac{1}{24}$ "	$\frac{1}{24}$ "	6	7
Part in broad ligament,	$\frac{1}{8}$ – $\frac{1}{2}$ "	$\frac{1}{8}$ – $\frac{1}{2}$ "	38	41
			<hr/> 51"	<hr/> 57"

The funnel-shaped beginning of the tube, $\frac{3}{4}$ –1 inch in length, leads from the ostium abdominale to a narrow sinuous tube placed behind the ovary between the two layers of peritoneum forming the ovarian sac. At the commencement of the broad ligament this tube becomes extremely narrow ($\frac{1}{24}$ inch), and insinuates itself among the muscular tissue of the broad ligament, coursing along the ovario-fallopian ligament. Thus far the tube is provided with no proper muscular coat.

In the broad ligament proper, the tube courses backwards near, but not quite at, the edge of the ligament. It is invested by a loose muscular sheath, which is not at all definitely marked off from the muscular tissue of the rest of the broad ligament. The muscular wall is most definite about the middle of the tube, where it is about $\frac{3}{4}$ inch in width. As it approaches the middle line, the tube leaves the border of the broad ligament, and passing backwards mesially, joins the opposite tube in the middle line 9 inches from the attached border of the broad ligament, to form the body of the uterus (figs. 1, 7, Co. Ut.). The part of the tube that recedes from the surface is placed between two broad sheets of muscular fibres, and has no distinct and separate muscular wall. At first very narrow, this part of the tube gradually dilates as it approaches the middle line, its diameter being $\frac{1}{8}$ inch at the beginning, $\frac{1}{2}$ inch at the termination.

THE UTERUS.¹

The uterus is naturally divisible into two parts: (1) *the corpus uteri*, in the broad ligament; (2) *the cervix uteri*, in the space between bladder and rectum.

¹ In removing the pelvic viscera, the mesial part of the base of the broad liga-

1. *In the broad ligament*, by the junction of the two Fallopian tubes, a narrow thin-walled tube is formed (corpus uteri) (figs. 1, 7, Co. Ut.) 4 inches in length and $\frac{1}{2}$ inch in diameter. It widens out towards its termination. At its commencement it is joined by the two Fallopian tubes without any change in the character of the tube, the interior of which is uniformly smooth. It is loosely covered in front and behind by a double sheet of muscular fibres, which is continued over the front and back of the second part of the organ (figs. 1, 2, 3, Ce. Ut.).

2. *Between the rectum and the bladder* the uterus is larger and more capacious (cervix uteri). It is a tube 7 inches in length, and is directed forwards and downwards to the os uteri (fig. 3, Os.). It is narrow, and less than 1 inch in diameter at its commencement, but expands below so as to be nearly 3 inches wide at its termination. Its wall is thick, and composed of dense fibrous tissue. The interior of this portion of the uterus, at first narrow and smooth, is soon thrown into irregular longitudinal folds, permanent in character. These folds are small above, and enlarge as they descend towards the os uteri. They end below by entering into the formation of the lips of the os uteri. Surrounding the whole of this part of the uterus in front and behind are two sheets of muscular fibres, continued from the broad ligament. These fibres are pale in colour, and extend as far as the beginning of the vagina, where they become continuous with the longitudinal muscles of the vaginal wall. Under these strata the lower portion of the uterus has a continuous investment of pale muscular fibres of considerable thickness.

The os uteri is a thick fleshy ring which projects into the lumen of the tube, and forms a definite separation between uterus and vagina. It projects for $\frac{1}{2}$ to $1\frac{1}{2}$ inches all round, and has a very irregular free margin, provided with seven flat, thick projections: the uterine aspect of the ring receives the ends of the uterine folds, while the vaginal surface is uniformly smooth.

ment was divided, so cutting across the uterus at the point where it passes between rectum and bladder. There does not appear to have been any loss of material: the two ends of the organs fit into one another, completing the continuity of the tube. •

THE VAGINA.

The vagina (figs. 1, 2, 3, Va.) is a capacious tube, which extends obliquely downwards and forwards beneath the bladder and urethra to the hymeneal orifice, at the beginning of the urogenital canal. It is placed above and in front of the rectum and the perinæal tissue; laterally it is related to the levator ani, and is invested by the bulbo-cavernosus muscle. The vagina is $19\frac{1}{2}$ inches in length, tapering in form, and with a varying diameter in different parts of the tube. At the os uteri it is nearly 3 inches wide; in the middle of its length it narrows gradually to $2\frac{1}{2}$ –2 inches; 3 inches from its termination its diameter narrows to 1 inch; and it is finally limited by the membranous folds of the hymen, which cause the termination of the vagina to assume a conical form, ending in a narrow vertical slit $\frac{1}{4}$ inch in depth (fig. 3, Hy.). The wall of the vagina is clothed by pale muscular fibres, continuous with the muscular sheets investing the anterior and posterior surfaces of the uterus, and derived from the broad ligament.

THE UROGENITAL CANAL.

The urogenital canal (figs. 2, 3, Ug. C.) is a tube of varying calibre, extending downwards and forwards from the openings of the urethra and vagina to the vulva. This canal is 3 feet in length. Its diameter just beyond its commencement is $1\frac{1}{4}$ inches: at a distance of 10 inches from its commencement it is 3 inches wide. It again becomes constricted to $1\frac{1}{4}$ inches, and then gradually widens in its lower two-thirds, becoming $4\frac{1}{2}$ inches wide at the vulvar orifice (from the base of the clitoris to the posterior margin). The proximal two-thirds of the tube are thus fusiform in shape, narrower at the ends than in the middle. The terminal third, which is in relation to the body of the clitoris, is cylindrical, and dilates near its termination to form a funnel-shaped opening underneath the clitoris.

Mucous membrane.—The lining of the tube is of a reddish colour, and in general is almost smooth. There are upon it a series of fine ridges, collected into two main longitudinal series

on the dorsal and ventral walls respectively. At the sides of the tube they become oblique, and more scattered and irregular.

Openings in the Mucous Membrane. 1. *Urethra*.—At the beginning of the canal are two openings—that of the urethra above, that of the vagina below. The urethral orifice (figs. 2–5, Ure.) is a round thick-lipped aperture, $\frac{3}{4}$ inch in diameter. The lip is specially prominent at its posterior or lower part, where it overhangs the vaginal opening. From this thick margin five broad prominent ridges (figs. 4, 5, *f*) radiate outwards into the wall of the urogenital canal, on which they gradually fade away. They have no great extent, and are reduplications of the mucous membrane. One ridge is mesially placed in the mid-dorsal line, above the urethral orifice, and there are two on each side. By these prominent folds five pouches are formed,—two blind pouches on either side and a single median depression in the mid-ventral line, in which the hymen and vaginal orifice occur.

2. *Vaginal orifice*.—This aperture (figs. 3, 4, 5) occupies the lowest median depression below the urethral orifice, at the commencement of the urogenital canal. The pouch leads into three orifices, of which the central one is the vaginal opening, the two lateral ones being blind pouches on either side. The vaginal opening is a very narrow vertical slit $\frac{1}{4}$ inch in length, formed by the margins of the hymen (Hy.).

The Hymen consists of two oblique translucent folds of mucous membrane attached to the vaginal wall, and projecting forwards into the beginning of the urogenital canal. The right fold is $1\frac{1}{4}$ inch, the left fold 1 inch in length. Each has a free straight anterior edge, $\frac{1}{2}$ inch in depth, attached separately to the floor of the pouch. The upper part of each edge is fused with its neighbour, so as to reduce the orifice to a narrow cleft $\frac{1}{4}$ inch in depth. The vaginal surfaces of the hymen are smooth, and continuous with the lining membrane of the tube, so as to give no indication of its presence on that aspect. In relation to the urogenital canal, they form the inner boundaries of a fossa on either side of the hymeneal slit. Each is a blind pouch, $1\frac{1}{4}$ inches deep on the right, 1 inch on the left side, with an oval aperture $\frac{1}{3} \times \frac{1}{4}$ inch in extent, opening into the commencement of the urogenital canal.

3. *Ducts of Bartholin's glands (?)* (figs. 2, 3, 5, Bar.).—The

three openings of these ducts are in the floor of the urogenital canal, $\frac{1}{2}$ inch from the middle line on either side. Each opening is oblique and $\frac{1}{4}$ inch in diameter. There are two ducts on the left side, one on the right side. The opening of the right duct is $1\frac{1}{2}$ inches behind the junction of the crura clitoridis, 16 inches from the commencement of the tube. The openings of the left ducts are 2 inches apart, 15 and 17 inches from the commencement of the tube, the anterior opening being just behind the junction of the crura clitoridis. These ducts, which have extremely thin walls, after piercing the membranous wall of the urogenital canal, are directed backwards beneath the erectile tissue and muscular coat. Entering the erectile tissue, they terminate there after dividing into narrower and narrower tubes. They do not pass through the muscular coat, and, as far as can be made out, are not connected with any glands. The length of the main duct on the right side is 7 inches; the anterior duct of the left side is $8\frac{1}{2}$ inches long, the posterior duct $7\frac{1}{2}$ inches.

The Erectile Tissue of the Urogenital Canal—(fig. 9, Er.).—A continuous layer of spongy erectile tissue surrounds the mucous membrane of the urogenital canal, beneath the muscular stratum. Mingled with it and continuous with it is a thin sheet of muscular fibres. It is a layer of considerable thickness in relation to the posterior two-thirds of the tube, but becomes much thinner anteriorly, except on the dorsal wall. It is greatly thickened on the dorsal wall of the tube beyond the point where the crura clitoridis unite to form the corpora cavernosa. It closely attaches the united crura, and binds down the under surface of the corpora cavernosa to the dorsal wall of the tube, and serves as a corpus spongiosum (C. Sp.).

The Clitoris (figs. 1, 2, 3) is formed by the junction of two crura to form a united pair of corpora cavernosa, connected on their under surfaces with the thickened mass of erectile tissue on the dorsal wall of the urogenital canal. It is 19 inches long, and is continued forwards to the glans clitoridis, beneath the tendon of the levator clitoridis. The sides of the corpora cavernosa give origin to the bulbo-cavernosus muscle. Surrounding each corpus cavernosum is a thin layer of muscular fibres (*ischio-cavernosus*?), beneath which is erectile tissue.

The Muscles of the Urogenital Canal.

Pelvic fascia.—A very tough layer of fascia closely encircles the neck of the bladder and the vagina, and is continuous behind with a sheet of fascia passing across the middle line in front of the rectum. It gives origin inferiorly to the posterior fibres of the bulbo-cavernosus muscle.

The muscles associated with the urogenital canal are four in number—bulbo-cavernosus, ischio-cavernosus, levator ani, and erector clitoridis. There is also present a separate sphincter ani externus.

The Bulbo-cavernosus (fig. 1, B.C.) forms a complete investment for the urogenital canal outside the erectile tissue of its wall. 1. Posteriorly, three irregular slips form its commencement, arising from the pelvic fascia (B.C. 1), and passing forwards round the rectum to embrace the urethra and vagina. These fibres are continuous above with the sphincter of the bladder, but are clearly distinguishable from it. 2. Continuous with these fibres is a tubular sheet of muscle (B.C. 2), encircling the urogenital canal as far as the point of separation of rectum and urogenital canal. 3. At this point fibres of the levator ani (L.A.) reinforce the bulbo-cavernosus muscle in two bundles: (1) the higher extending round the urogenital canal in continuous series with those above named; (2) the lower fibres passing forwards to be continuous with the next series of fibres. The two series are separated on the wall of the urogenital canal by the crus clitoridis, passing forwards to form the corpus cavernosum.

4. Beyond the junction of the crura to form the clitoris, the bulbo-cavernosus arises from its sides in a continuous sheet (B.C. 3). Sweeping ventrally round the urogenital canal, the posterior fibres blend with fibres of the levator ani (3), the intermediate fibres extend transversely round the canal, and the anterior fibres, much thinned out, are directed obliquely forwards, so as to form the muscular wall of the genito-urinary sinus (vulva).

Posteriorly, this muscle is of considerable thickness. Anteriorly, it is much thinner, and becomes inextricably blended with the subjacent erectile tissue. It is supplied by large branches of the pudic nerve.

Ischio-cavernosus.—The only trace of this muscle was in the form of a thin layer of muscular fibres surrounding each crus clitoridis on its way to form the clitoria.

The Levator ani (L.A.) appears to exist in two parts:—

A. *Upper part* (larger).—A considerable band of muscular fibres, the origin of which was cut (it appeared to come from the lower sacral vertebræ), passes forwards alongside the rectum, and is inserted in a fourfold manner. 1 and 2. As already mentioned, the highest part of the muscle subdivides into two sheets (separated by the crus clitoridis), which join parts of the bulbocavernosus, and are inserted into the urogenital canal. 3. A third portion of the muscle below these is inserted into the perinæal fascia in front of the rectum. 4. The lowest and largest set of fibres sweep downwards on to the rectum, and become continuous with its longitudinal muscular coat.

B. *Lower part* (smaller).—The posterior attachment of this portion was also divided. It is a broad band of muscle which, passing forwards on the side of the rectum, is inserted in three portions. 1. The highest fibres pass forwards round the rectum so as to embrace it anteriorly, outside the longitudinal muscular coat. 2. An intermediate set of fibres passes in front of the rectum to the fascia of the perinæum. [This layer was cut anteriorly. It appeared to have an insertion into the perinæal fascia.] 3. The lowest fibres, in two bundles, pass downwards along the rectum, and become continuous with the longitudinal muscular coat. The muscle is supplied by branches of the pudic nerve.

Sphincter ani externus (S.E.) is imbedded in the fascia alongside the anus; it was divided at each end. It consists of an elongated cylindrical muscle, extending antero-posteriorly around the anus and alongside the terminal portion of the rectum. It is supplied by the pudic nerve.

The Levatores clitoridis (L.Cl.) were divided at their origin. The muscular bellies are long and cylindrical, and anteriorly form two narrow tendons, which join to form a single median tendon. This, after passing along the whole length of the dorsum of the clitoris, is inserted into the dorsum of the glans clitoridis. It is supplied by a branch of the pudic nerve.

EXTERNAL GENITAL ORGANS.

When the animal was received on the fourth day after poisoning by aconite, the external genitals were much swollen and distended. A fortnight later, when the sketch was made, they had become flaccid and wrinkled.

Vulva.—The vulva (fig. 10) is placed far forward, in front of and between the thighs, and projects slightly from the belly wall. The distance between the posterior margin of the vulva and the anterior margin of the anus is $24\frac{1}{2}$ inches. The opening of the vulva looks downwards and slightly forwards. It is oval in shape, and measures 9 inches antero-posteriorly, 6 inches from side to side. It is surrounded with sparse and scattered bristles, and itself is devoid of hair. It is in the form of two thick wrinkled lips (La.), united anteriorly by a mons veneris or prepuce (Pr.), and meeting behind in a thin sharp margin. The lips present several grooves, and numerous smaller irregular wrinkles radiating from the interior. Within these lips are the genito-urinary orifice and the glans clitoridis (Gl. Cl.).

The genito-urinary orifice, directed downwards, and slightly forwards, is oval in shape, and admits the closed hand when folded into a conical shape. Within it the wrinkled epidermis of the vulva is suddenly transformed into the smooth lining of the urogenital canal. The passage widens just within the orifice. For a distance of 4 inches, just behind the orifice, is a series of wide openings of minute glands in the floor of the canal.

The glans clitoridis is placed in front of the genito-urinary orifice, and overhangs it. It measures 3 inches both in length and width, and has a free extremity bifurcated for half an inch in the centre. The prepuce forms a kind of hood over its dorsal surface; its lateral margins are prolonged into folds forming fræna (Fr.). It is flattened from above downwards, and on its upper surface has a tongue-shaped projection in low relief, making a kind of third lobe. The under surface of the glans is covered by smooth skin, continuous with the lining of the genito-urinary passage. Its dorsal surface is covered with wrinkled dark-coloured epidermis. At the junction with the prepuce the cutaneous wrinkles are particularly fine.

GENERAL OBSERVATIONS.

Several points of anatomical and physiological interest arise from a comparison of these observations with those of others, notably in relation to the genital tract of the female elephant.

I. *Urinary Organs.*—*The Kidneys* resemble in all essential points those previously described. The dimensions and weight, though greater, are similar in proportions, if Stukeley's case (16), where the length of the kidney was 3 ft., is excepted. The lobulation is similar to previous cases in being present only upon the ventral surface. The number of lobules described is very variable: Mayer (9), 2; Cuvier, 4;¹ Watson (20), 4, 5, 7; Forbes (5), 8; Hyrtl, 9;¹ Von Mojsisovics (11) and Dönitz (3), 10. The position of the hilum on the ventral surface agrees with previous observations.

The Ureters arise from superior and inferior groups of calices in our case as in Mayer's (19); from anterior and posterior groups in Miall and Greenwood's (10) and Watson's case (20). The course and relations have not been previously noted, except in Watson's case (20). The opening into the bladder has been similarly described by previous observers.

The Bladder in its shape and relations agrees with previous descriptions. The muscular coat was thick in Mojsisovics' (11) and our own case; the submucous coat relatively thicker than the muscular in Watson's specimen (20).

Our account of the Urethra agrees with previous descriptions.

II. *Generative Organs.*—*The Ovary* resembles in all essential features the description and figures of Chapman (1), Forbes (5), Mayer (9), Miall (10), and Watson (17).

The Fallopian tubes and *uterine cornua* are peculiar in two respects:—(1) There is not that abrupt and definite demarcation of Fallopian tube from cornu in our specimen that is shown in the examples of Chapman, Forbes, Mayer, Miall, and Watson. While the part of the tube in relation to the ovario-fallopian ligament is extremely narrow ($\frac{1}{24}$ inch), it blends *gradually* with the portion of the tube contained within the broad ligament proper, and is not to be distinctly separated into fallopian tube

¹ Quoted by Dönitz (3).

and uterine cornu. (2) The other feature of these tubes is their extreme length (R. 51, L. 57 ins.). In Chapman's example (1), the height and age of the elephant are not given; but the length of the urogenital canal (36 ins.) indicates that the animal was of considerable size. The cornu and Fallopian tube in his case measured only 32 inches—the same length as in Perrault's case (14)—(an African elephant $8\frac{1}{2}$ feet high and eighteen years of age). The other animals dissected have been much younger and smaller, but in all the Fallopian tubes and uterine cornua have been very much shorter in proportion to the total length of the genital apparatus.

The *uterus* presents certain distinctive characters:—(1) it is unilocular; (2) it is separated into corpus and cervix uteri; (3) it is separated from the vagina by a distinct os uteri.

(1) The presence or absence of an intra-uterine septum appears to be a matter of the greatest variability. Of the uteri of three African elephants, two (Perrault's (14) and Chapman's (1)) examples are unilocular; one (Forbes's (5)) is provided with an incomplete septum, $4\frac{1}{2}$ inches in length, dividing the corpus uteri into two parts. Of the uteri of seven Indian elephants, four (Hunter's (8), Mayer's (9), Miall's (10), and our own) examples are unilocular; three (Watson's two cases (17, 18) and Stukeley's (16)) are provided with partial or complete septa. Altogether, four examples are provided with septa; six are unilocular. Further, in three cases there is an intra-vaginal septum in one form or another. In Watson's first case (17) there is a completely double uterus and vagina. In Stukeley's case (16), while apparently the os uteri is the mouth of a single cavity, and the intra-uterine septum is almost complete, the vagina is again partially separated into two by an independent septum in its lower part. In Miall's case (16) the uterus is unilocular, and the vagina is a simple canal; but its external orifice "is divided into lateral halves by a thick rounded cord covered by mucous membrane, which is apparently a hymen." This cord may, in the light of other cases, and in virtue of the fact that another structure representing the hymen appears to exist, be rather regarded as a rudimentary intra-vaginal septum.

(2) Although we are ignorant as to what part of the uterus is occupied by the embryo, it is important to point out that the

uterine cavity is distinctly separable into corpus and cervix. The *corpus uteri*, occupying the broad ligament, is narrow and smooth in its interior; the cervix, lying below the broad ligament, is much more capacious, and has its mucous membrane thrown into longitudinal folds terminating below at the os uteri. In all previous observations (except Watson's (17)) the lower part of the uterus is unilocular. Miall, however, is the only observer who has previously referred to a dilated lower part, and referred to it explicitly as cervix.

(3) The character of the os uteri is apparently very variable. In this case it was prominent and circumferential. In Miall's case it was in the form of anterior and posterior crescentic projections. In Watson's first case (17) it was in the form of two similar lateral projections. In his second case (18) it was "a slightly puckered constriction admitting the passage of a finger." It appears to be generally present in some form or other, making a clear division between uterus and vagina. The Indian elephant is therefore not exceptional in this respect, but resembles other mammals, and differs from *Hyena crocuta* (21). The vagina is clearly demarcated from the uterus by the os uteri, and from the urogenital canal by what we have ventured to call the *hymen*. This external orifice of the vagina has been described in detail, as there are extraordinary differences in the accounts of previous observers. Hunter, who calls the urogenital canal "the common vagina, which is common to the urine and penis," and the vagina proper, the "uncommon vagina, where the penis cannot enter," states that "at the termination of the proper vagina its cavity contracts at once almost to a blind end, in the centre of which there are three small openings, neither of them larger than a crow-quill; the two lateral of these lead to two small sacs, which pass a little way along the sides of the common vagina. The urethra opens into the very beginning or fundus of the common vagina; the middle orifice leads into the uncommon vagina, which soon dilates." This account only differs from ours in the fact that the openings of the lateral pouches on either side of the vaginal orifice are directed apparently towards the vagina, instead of towards the urogenital canal. Forbes and Watson describe the pouches exactly in the position of those in our case; the latter compares them to Gartner's ducts. He describes a

cushion of mucous membrane separating urethral and vaginal openings. Perrault figures two sigmoid valves, and a valve-like fold separating urethra and vagina. This agrees with Chapman's description, which states that the vaginal openings "can be completely cut off from the urogenital canal by a valvular fold of mucous membrane, of somewhat semilunar shape, about $2\frac{1}{2}$ inches in breadth. The effect of this fold appears to be to prevent the flow of urine into the vagina." Mayer does not describe the lateral pouches, but figures the cushion and lateral folds between urethra and vaginal orifices. Miall describes neither fold nor pouches. In our own case there is between the urethral and vaginal openings a structure which might be described as a cushion with lateral folds, but no distinct flap or valve, and on either side of the vaginal openings two blind pockets are formed by the valvular folds of the hymen. These are intra-vaginal, and do not pierce the wall of the tube. Owen (8, 13) has described these pouches as the "mucous sinuses or canals of Malpighi," while Watson (17) has asserted them to be the ducts of Gartner. Both these terms apply to the same thing—a remnant of the Wolffian duct. They are, however, really sinuses or pouches formed by the cusps of the hymeneal valve (not described by previous observers), and there is no representative of the Wolffian duct present. The particular interest of this series of structures will be referred to again. If the folds referred to constitute the hymen, it is hard to believe that the vagina is not entered by the penis of the male, as the valvular arrangements at the beginning of the urogenital canal appear to be specially devised for the purpose of preventing the entrance of all fluids into the vaginal canal.

The muscles of the urogenital canal have necessarily been only imperfectly described in the foregoing pages, as their pelvic attachments were to such an extent divided. What we have described as *levator ani* corresponds apparently to the external sphincter of other observers. In their cases (*e.g.*, Watson's (17)), the true external sphincter had been cut away, whereas in our case it is present along with this muscle, which appears to have, from its insertions, a considerable influence in drawing upwards and backwards the urogenital canal, perinæum, and rectum, and so helping to bring the vulva in near proximity to the anus.

The bulbo-cavernosus muscle, by its attachments, would appear to aid in the retraction of the urogenital canal; and by its anterior fibres, in the eversion of the edges of the vulva.

The position of the vulva in the elephant has led to the formation of all kinds of absurd views as to the position of the animals in sexual intercourse. In our specimen it was placed 2 feet in front of the anus, and in front of and between the thighs. There appears to be not only a possibility but a certainty that in the act of copulation the two animals occupy the usual quadrupedal position. The action of the levator ani, levatores clitoridis, ischio-cavernosus, and bulbo-cavernosus muscles must have the effect of retracting and drawing backwards the urogenital canal, and bringing its lumen more into line with the rectum. Another question, however, is even more difficult. Is the elephant's vagina useless as a sexual organ? The examination of its opening into the urogenital canal has shown how difficult the passage of fluid would be, so long as the hymen is intact. One doubts if John Hunter's dictum can be accepted, that the vagina is the uncommon vagina, into which the penis cannot enter. It is not known in what part of the uterus the embryo is developed; and there is no authentic account of the dissection of the generative apparatus of a female elephant that has borne young. The only evidence on which one's views can be based is also very unreliable, viz., the length of the penis. The length of the urogenital canal in our case was 36 inches; the greatest length recorded is in Perrault's case (14), 42 inches. There have been recorded three observations regarding the length of the penis: Du Vernoi (4) described one weighing 80 lbs., and 6 feet long; Suply (reported by Stukeley (16)) describes one as 48 inches in length, from an animal 7 or 8 cubits high. In Watson's example (20) the length of the penis was 30 inches, the height and age of the animal being not stated.

Putting all these considerations together, one concludes that it is more than possible that impregnation may require penetration of the vagina by the male organ, and the destruction of the barrier formed by the hymen.

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EXPLANATION OF PLATES XIV., XV.

Fig. 1. Pelvic viscera and muscles; $\frac{1}{10}$ natural size. *B.L*, broad ligament. *Co. U*, corpus uteri. *Ur.*, ureter. *Bl.*, bladder. *Ce. Ut.*, cervix uteri. *Va.*, vagina. *Sph. V*, sphincter vesicæ. *R*, rectum. *L.A*, levator ani. *S.E*, sphincter externus. *B.C*, 1, 2, 3, bulbo-cavernosus. *U.G.C*, urogenital canal. *L. Cl.*, levator clitoridis. *Cl.*, clitoris. *An.*, anus. *Per.*, perinæal tissue. *Vu.*, vulva.

Fig. 2. Bladder, urethra, and genital passages (muscles removed); $\frac{1}{10}$ natural size. *Ure.*, urethra. *Bar.*, Bartholin's glands.

Fig. 3. Bladder (*Bl.*), rectum (*R*), and genital passages in mesial section; $\frac{1}{10}$ natural size. *Ur.*, ureter. *Hy.*, hymen. *Os*, os uteri. *Gl. Cl.*, glans clitoridis. *Ure.*, urethra.

Fig. 4. Semi-diagrammatic representation of fundus of urogenital canal; $\frac{2}{3}$ natural size. *f* 1-5, folds passing from urethral opening (*Ure.*). *Va.*, placed below vaginal opening. *Hy.*, placed on folds of hymen. The arrows point to the pouches (Malpighian ducts ?) on either side of hymeneal folds.

Fig. 5. Dorsal (posterior) aspect of bladder, and floor of urethra and urogenital canal; $\frac{1}{8}$ natural size. *Va. O*, placed below vaginal opening: pouches on either side.

Fig. 6. Broad ligament (*B.L*). *Ut.*, uterus. *R*, rectum. *Or*, placed at hilum of ovary. *O.F.L*, ovario-fallopian ligament. *D.l.*, diaphragmatic ligament. *S*, ovarian sac. *I*, Infundibulum. *Ost.*, ostium abdominale. *Sec.*, secondary folds of broad ligament. $\frac{2}{3}$ natural size.

Fig. 7. Dissection of the broad ligament. *M.M*, muscular strata (cut). *Co. Ut.*, corpus uteri. *F.T*, Fallopian tube. *O.F.L*, ovario-fallopian ligament. *D.L*, Diaphragmatic ligament. *Ov.*, ovary. *S*, ovarian sac. *I*, Infundibulum. *O.A*, ovarian artery. $\frac{2}{3}$ natural size.

Fig. 8. Comparison of observations on the genital tract of the elephant. *A*, Forbes. *B*, Chapman. *C*, Perrault. *D*, Watson (1). *E*, Watson (2). *F*, Miall and Greenwood. *G*, Mayer. *H*, Stukeley. *I*, Paterson and Dun. *J*, Hunter. $\frac{1}{8}$ inch to foot.

Fig. 9. Diagrammatic transverse section of urogenital canal. *M.M*, mucous membrane. *C.C*, corpus cavernosum clitoridis. *C. Sp.*, corpus spongiosum. *Er.*, erectile tissue. *B.C*, bulbo-cavernosus.

Fig. 10. Vulva; $\frac{1}{4}$ natural size. *Pr.*, prepuce. *Gl. Cl.*, glans clitoridis. *Fr.*, fræna. *La.*, labia.

Fig. 11. Left ovary (*Ov.*); $\frac{2}{3}$ natural size. *S*, ovarian sac. *I*, Infundibulum. *Ost.*, ostium abdominale. *Hi.*, ovarian hilum. *O A*, *O V*, ovarian vessels.

Fig. 12. Left kidney; $\frac{3}{10}$ natural size; ventral surface, with hilum. 1, superior; 2, anterior superior; 3, anterior inferior; 4 and 5, inferior; 6, posterior inferior; 7, posterior superior lobe. *Art.*, renal artery. *V.V*, renal veins. *Ur.*, ureter.

Fig. 2.

Fig. 4.

f^1

f^2

v_1

v_a



1

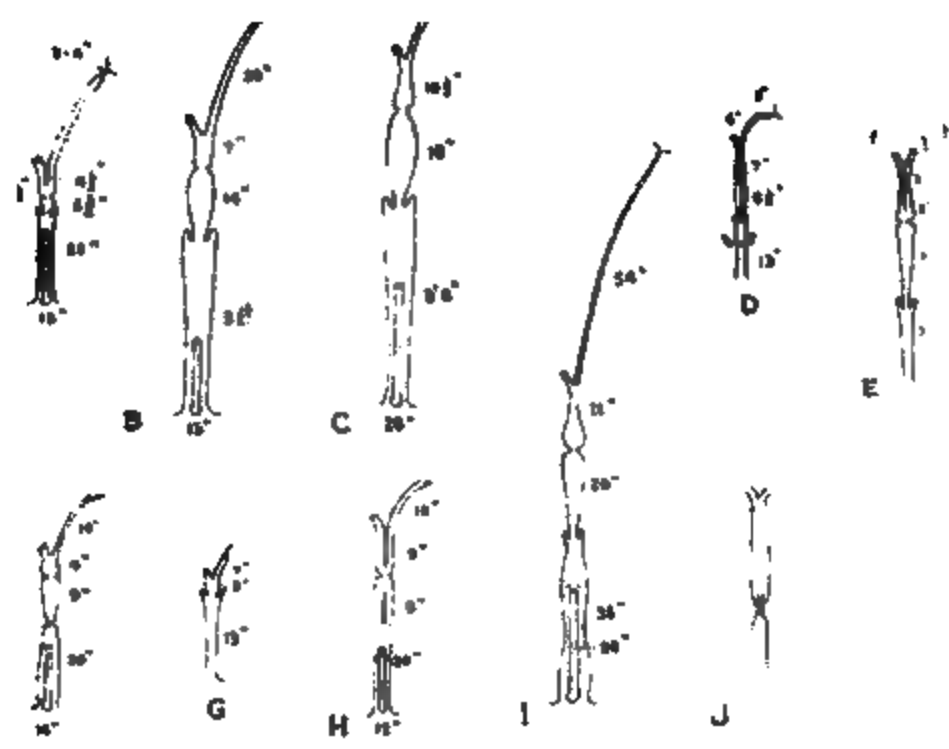
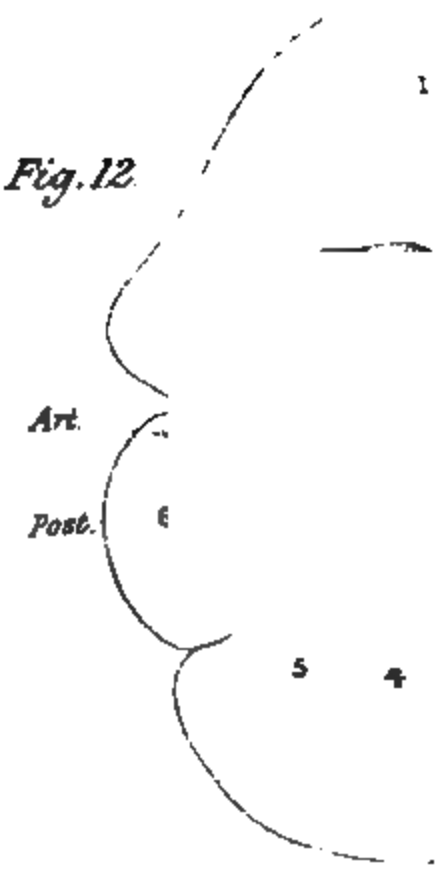


Fig. 12.

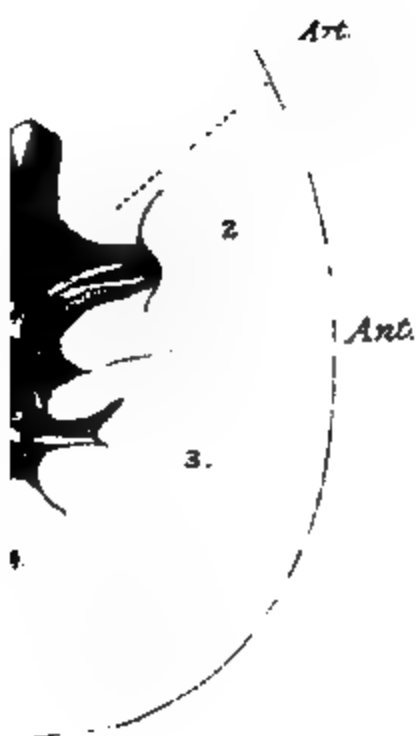


A R.C.D. del

Fig. 16

Ost.

I.



THE DEVELOPMENT AND MORPHOLOGY OF THE VASCULAR SYSTEM IN MAMMALS. THE POSTERIOR END OF THE AORTA AND THE ILIAC ARTERIES.¹
By ALFRED H. YOUNG, M.B., F.R.C.S., and ARTHUR ROBINSON, M.D. Communicated by Sir WILLIAM TURNER, F.R.S.

THOUGH numerous observations have been made on the development of the systematic aorta and on the aortic arches, including their modifications and transformations at the head end of the embryo, but little attention has been given to the development and modifications of the primitive vessels and the aortic arches at the caudal end.

The statement that the primitive aortæ are prolonged backwards from the dorsal region into the tail, and that, fusing there, they form a caudal aorta—the middle sacral artery—seems to be generally accepted by embryologists. Obviously, if this view is correct, the iliac arteries are not formed from, and do not represent any part of, the primitive aortæ, and they are generally regarded as being segmental in character.

Previous observations on the comparative anatomy of the mammalian aorta and its terminal branches made by one of ourselves in 1891, seemed to show that the true posterior continuation of each primitive dorsal aorta was to be found, not in the middle sacral artery but, in the iliac and hypogastric trunks. It was impossible, however, to arrive at any satisfactory conclusion on the question in the absence of definite and precise information regarding the development of the caudal end of the aorta and its branches.

We therefore commenced a series of observations on the development of the posterior parts of the main systemic vessels in the rat, mouse, ferret, cat, and sheep. In the first three of these the sections examined represent a fairly complete series of the early stages of development. In the cat several embryos of two different stages were referred to, whilst our sections of sheep embryos represented only one stage of development.

In our description of these the embryos of each class are arranged in groups according to the stage of development of their arterial systems, and in each group the general stage of development is indicated by a short statement of the condition of some of the main organs.

On developmental grounds alone the following conclusions, which form a brief summary of the results of our observations, have been arrived at:—

1. The primitive aortæ are paired trunks which pass at either end of the embryonic area into the vascular network on the wall of the yolk sac.

¹ Abstract of a paper read to the Royal Society of London, 10th February 1898.

2. With the formation of the cephalic and caudal folds each primitive trunk, at first almost straight, is so folded in front and behind that a dorsal and two ventral portions with uniting caudal and cephalic arches are differentiated.

3. The dorsal part of each trunk is modified in the cephalic region into vessels of the head and neck; the remainder of each dorsal portion fuses with its fellow of the opposite side to form the greater part of the systemic aorta.

4. The cephalic or anterior ventral portions are converted into the heart, the ventral part of the arch of the adult aorta, and vessels of the head and neck.

5. The caudal or posterior ventral portions either fuse together to form a common vitello-allantoic stem, as in rodents, or they remain separate and form the ventral parts of the allantoic arteries as in carnivores, ruminants, and man.

6. The ventral and dorsal sections at first are united anteriorly by a cephalic arch and posteriorly by a primary caudal arch. Additional cephalic arches are developed subsequently, to be afterwards utilised in the formation of vessels of the head, neck, and upper extremity, and of part of the arch of the aorta of the adult, whilst additional arches in the caudal region may also be formed, to be utilised as visceral arteries.

7. The dorsal and ventral extremities of the primary caudal arches remain; the dorsal extremities take part in the formation of the posterior end of the aorta of the adult; the ventral extremities are utilised in the formation of the ventral portions of the allantoic or hypogastric arteries.

8. The middle parts of the primary caudal arches disappear and are replaced by "secondary" caudal arches which lie to the outer sides of the Wolffian ducts. In rodents and man the secondary arches are transformed into the common and internal iliac arteries and the dorsal parts of the hypogastric arteries, whilst in carnivores they are probably transformed into the posterior part of the adult aorta and into the internal iliacs and dorsal parts of the hypogastric arteries.

9. The vessels, which are to be looked upon as the posterior continuations of the primitive aorta in the adult in man, rodents, etc., are the common iliac, internal iliac, and hypogastric arteries, and in carnivores, etc., the internal iliac and hypogastric arteries.

10. The common internal iliac arteries are not segmental vessels; their branches may be.

11. The middle sacral artery is a secondary branch, probably representing fused segmental vessels.

12. The systemic aortæ is formed from the following parts of the primitive vessels: the anterior ventral aorta, the fourth left cephalic aortic arch, the fused portions of the primitive dorsal aortæ, and in some mammals the fused dorsal ends of the caudal arches.

The permanent adult aorta, in so far as it is formed by the primitive dorsal aortæ, ends posteriorly either at the bifurcation into the two common iliac arteries or at a point corresponding to this bifurcation, when by more extensive fusion involving the dorsal parts of the

secondary arches there are no common iliacs, and the external and internal iliac arteries appear to arise directly and separately from the aorta. In each case the continuity of the primitive aorta is interrupted, and the primary caudal arches are replaced by secondary caudal arches, after which the continuations of the aorta are represented by the vessels into which the secondary caudal arches are ultimately transformed.

These conclusions are further supported by more extended observations on the anatomy of the posterior end of the aorta, and its terminal branches in mammals, and on the abnormalities they present in man, a general account of which is included in the memoir.

Notices of New Books.

Traité des Variations de Système Musculaire de l'Homme, et leur Signification au Point de Vue de l'Anthropologie Zoologique. By Professor A. F. Le DOUBLE. Paris: Schleicher Frères. 1897.

Muskeln und Periphere Nerven der Primaten, mit besonderer Berücksichtigung ihrer Anomalien. By Dr I. H. F. KOHLBRUGGE. Amsterdam: Müller. 1897.

THE literature of the muscular system in man and other vertebrates is extensive but unsatisfactory. It consists chiefly of the records of dissections, described with more or less accuracy; but concerning the embryology of the system it is almost perfectly blank. The medical student spends nearly half the time that he allots to dissection in cleaning and preparing the muscles of the body; but these structures have been passed over with but scant attention by the embryologist,—indeed there is scarcely a muscle in the body whose history has been fully worked out. It is therefore impossible in the present state of knowledge to interpret with any degree of definiteness the ontological phenomena which have been described.

The variations presented by the muscles of man are numerous and easily observed, hence they furnish a happy hunting ground for the younger anatomist, and it must be confessed that the literature of this subject deserves the criticism passed on it by Professor Cleland as “being very praiseworthy, interesting to the recorder, very dry to most other people, and hitherto, so far as I am aware, barren enough of any conclusions. So much the more credit is due to those who have worked steadily, in faith that beauty will emerge to gild their results some day.”

Even from a purely descriptive standpoint the records of muscular anomalies are often unsatisfactory; it is only in the later literature of the subject that the relation of the nerve-supply to the muscle has been recorded; in the majority of records this, which, in the absence of embryological knowledge, is almost the only morphological criterion, is not noted. In this connection Kohlbrugge remarks with much truth that the descriptions of muscles without their nerves are of very little value.

Notwithstanding these imperfections in our knowledge, it is important for the anatomist that he should know what variations have

been hitherto described. The patient and painstaking researches of Professor Le Double have in these volumes put within our reach an easy guide to the prodigious literature of this subject. The learned Professor of Anatomy in Tours, well known to all anatomists as the author of many papers on this subject, has put us under a deep obligation by giving us in the 884 pages of his two large volumes a remarkably full bibliography and description of almost all the variations of the muscular system which have been published up to date. Life is too short for most of us to do much of this sort of work for ourselves, so our debt to him is all the greater. Only those who have tried to do a little labour in this field can have an adequate appreciation of the stupendous toil involved in the gathering out of the multifarious and polyglot literature of the last three centuries all the references to these anomalies. This task he has well done, for not only has he verified his references and quoted as far as possible at first hand, but in cases in which there are obscurities in the works of living anatomists he has endeavoured to obtain from the authors additional details. This book should be in the library of every practical anatomist, and in the laboratory of every anatomical school for purposes of reference. Until the time comes when the embryology of the muscular system has been investigated, it is likely that this book will remain the standard work on the subject. It is to be regretted that Professor Le Double has not given, at least as synonyms, the names of the muscles proposed by the international committee. It renders reference more difficult if we have to look out for each muscle under an unfamiliar vernacular name. This difficulty is, of course, only felt by foreign anatomists, the French habit being to use French names, a practice which very much interferes with the use of French books of anatomy in this country; and now that the largest number of the anatomists of the civilised world have agreed on a common system, it is desirable that all should adopt it, at any rate as a system of synonyms. The first function of a nomenclature is to be a means of enabling others to know at once of what we are speaking or writing. In this connection we may observe, in reference to a recent attempt at revision of muscle names proposed in this *Journal*, that as it is impossible to frame an ideally perfect nomenclature, the best we can do is to use those names which are most widely known; and he who introduces a new system must expect to have his writings disregarded by those to whom its unfamiliarity is a hindrance to their understanding his exact meaning. It is better to use an arbitrary nomenclature which is widely known, than a more perfect one only known to ourselves. This difficulty of understanding the meaning of names often interferes with our appreciation of the meaning of the older writers on account of their unfamiliar and faulty nomenclature, and in the work before us we have some illustrations of this. Thus in the case of the mass of the scaleni, Dr Le Double notes that before the eighteenth century it was described as constituting one muscle, then three were recognised, and now among the French writers only two are usually described. It is true that the father of modern anatomy, Vesalius, speaks of them

as one mass, the third muscle of the ribs, "*tertio a prima thoracis costa liberatoque, transversis cervicis vertebrarum inseratur processibus,*" but he figures separately the *scalenus anticus* in Pl. 8, C, and the hinder part of the mass in Pl. 14, N; he also speaks of it as split by the subclavian artery. Our author says that all anatomists after Riolan, except Chaussier, recognise the tripartite division, but this is scarcely accurate, for many, such as Blancard, Verheyen, Cheselden, Gibson, etc., speak of one *scalene* muscle. In the metrical myology of Sponius we read:—

In tereti octonos posuit cervice lacertos
Artificis motûs, solertis cura, Promethei.
Antrorsum collum bis-duplex flectere suetus,
Nimirum Longique duo, totidemque Scalenî.
Sublimant collum duo congeneris Spinatî.

And the same author in his poetical "crib" of the origin and insertion of the muscles says:—

Costâ Scalenus manat e primâ ordine,
Sursumque pergens, omnibus processibus
Transversa postis spondylôn colli ingruit.

At the same time, Cowper, Drake, and several others give the three muscles as at present described. He quotes Winslow as describing only two; but this author expressly says that the first is always, and the second sometimes, divided. Dr Le Double scarcely does justice to this anatomist in connection with the *scalenus pleuralis* by saying "*il a douté: il n'a pas su s'il avait bien vu.*" But Winslow's words are explicit (p. 237),—"paroissoit ensuite s'aller attacher a la voûte de la plevre."

These are, however, but minor matters, and only illustrate the difficulties of the task which Dr Le Double has executed so well.

The method of the work is simple: he takes each muscle, records all its varieties, and then gives a short account, with references, of those points in its comparative anatomy which illustrate the anomaly described. A work like this, dealing with references which are to be reckoned by the thousand, is not easy to read continuously; and the student will naturally turn to the last chapter, which treats of certain general considerations on the subject, such as the racial factor in anomaly, as indicated by the comparison of the statistics of varieties published in different countries: the relative frequency of variations in the muscles of different regions: the basis upon which a morphological classification should be founded: and the bearing of anomalies on the problem of atavism.

On the first of these subjects our knowledge is so scanty that little of definite value can be said, but all the available information is given here. With regard to the second, from the statistics given, it is clear that such parts as have the greatest range of diversity in use are those that show the greatest and most frequent variation, and *vice versa*.

In discussing the principle on which a classification of anomalies

should be founded, it is evident that this will depend on the hypothesis of causation which is adopted. Some authors regard the majority of anomalies as individualistic, arising from the action of the enviroing influences which affect the growth and development of the ovum. Others, like Professor Testut, regard almost all as due to atavism. Dr Le Double, while not taking such an extreme view, considers that the majority are due to reversion, and criticises the individualistic hypothesis as being unphilosophical, and as giving too much importance to individual environment. But some of the most characteristic muscular anomalies cannot be explained on this hypothesis,—for example, the rectus sternalis, which does not occur in any known mammal; so it is necessary to postulate a series of imaginary ancestors, unlike any known mammal, in that they possess this muscle, to bring it within the range of the hypothesis. Some anomalies are obviously local overgrowths; others are due to local interruptions of nutrition; others, such as transpositions of viscera, while admitting of an easy explanation embryologically, cannot be brought into the purview of atavism.

Before we can judge between these two theories, it is necessary that we should have a clear idea as to the meaning of atavism, which is here invoked as a causal force. Dr Le Double gives a number of definitions, but they do not help much; and it remains evident that the attribution of the causation of anomalies to atavism is an example of the argument from analogy, and is liable to all the fallacies which beset reasoning of that kind. The evolution hypothesis is itself at present undergoing an evolution, and out of the crude proto-Darwinism there is emerging a more philosophic and far-reaching theory, whose ultimate form it is impossible to forecast. What bearing the reconstructed theory may have on the hypothesis of atavism it is difficult to say, but there are some weighty words on the subject in a paper by Emery ("Homologie und Atavismus in Lichte der Keimplasmatheorie") in the *Biologische Centralblatt* for 1897, p. 344; and this author comes to the conclusion that it is an unproved assumption that the sporadic development of structures, of which there are no traces in the normal ontogenesis, can be attributed to atavism.

Dr Kohlbrugge, in his essay on atavism, published last year at Utrecht, carries this limitation of atavism still farther, and considers that the 'achselbogen' is the only muscular anomaly which may with any reasonable certainty be attributed to this cause. This, perhaps, is going to the other extreme.

The whole subject of variation is at present being considered by a Committee of the Royal Society, and we await their report with interest.

The work by Dr Kohlbrugge differs in scope and form from that of Dr Le Double. Its author is known as the writer of a monograph on the anatomy of the gibbons, which is a model of clearness and accuracy. In this essay he briefly reviews the muscular system of the primates, grouping the muscles according to their nervous supply, and taking as his basis of comparison the myology of *Semnopithecus* and

Hylobates, which he has had exceptional opportunities of studying. His work shows that muscular anomalies are as common among monkeys as in man, a fact known by all those who have opportunities of observing. Considering that Dr Kohlbrugge is a resident in Java, far from libraries and those other aids on which workers in European universities are accustomed to rely, the paper is remarkable, and will prove useful to those engaged in the comparative anatomy of man. It is probably due to the author's distance from the place of publication that the text is disfigured by many typographical errors.

The standpoint of Dr Kohlbrugge is exemplified by one of the concluding sentences of his paper on atavism, "Der alte Hyrtl sprach die prophetischen Worte":—"Es wird eine Zeit kommen, in welcher die Bedeutung der Varietäten der Muskeln besser verstanden sein wird, als jetzt, wo man sie nur als Curiositäten zu behandeln geneigt ist. Darwin's Lehre wird in den Muskelvarietäten, insofern sie Wiederholungen tierischer Bildungen sind, eine Hauptstütze finden. So geschah es auch, es folgte die Aera der phylogenetischen Betrachtung welche im Atavismus gipfelte: aber da heutzutage alles schnell wechselt, so ging auch diese vorbei. Eine neue Zeit bricht heran, die nach den Gesetzen der Variationen, nach der ontogenetischen Aus- und Umbildung, nach der mechanischen Nothwendigkeit fragt."

A. M.

EDITORIAL NOTE.

WHILE the Editors of this Journal do not intend to make any considerable change in its form or scope, they desire to effect certain improvements, especially in the matter of illustration, as they believe that the value of anatomical papers is enhanced when they are adequately illustrated. They hope that by extending this department the interest and value of the Journal will be commensurately increased. To enable them to meet the additional expenditure on the cost of production which this will render necessary, the Editors ask the co-operation of all who are interested in the progress of Anatomy and Physiology in extending the circulation of the Journal. They have learned that there are many public libraries in Universities and other scientific institutions in English-speaking countries in which the Journal is not taken, and not all those who are engaged in the teaching of these sciences are numbered among the subscribers; and they would respectfully ask all those who can help in this respect to

aid them in making this Journal a worthy representative of the progress of the science.

It is their intention to publish in each issue a record of the progress of some branch of these sciences,—not a mere list of the names and titles of papers, but a brief review of the contents of those that are of importance. In order to aid in the compilation of these reviews, the Editors request that authors will be good enough to send copies of their papers to the Publishers of this Journal, Messrs Griffin & Co., Exeter Street, Strand, W.C.

The Editors also intend to publish a series of papers dealing with the History of Anatomy and the cognate sciences, which it is hoped will prove of interest to those engaged in the study and teaching of these branches of knowledge.

The Council of the Anatomical Society have prepared complete Indexes of all the volumes of the Journal hitherto published, and similar Indexes will be periodically prepared, which cannot fail to be of use to those interested in Anatomical bibliography.

The Editors will spare no pains in doing their part in the work of the production of the Journal; but they wish it to be distinctly understood that they disclaim all responsibility for the matter or opinions set forth in the several communications which are published.

Communications for the Journal may be sent to any member of the editorial staff.

Journal of Anatomy and Physiology.

THE SALIVARY DIGESTION OF STARCH IN SIMPLE AND MIXED DIETS: AN EXPERIMENTAL INQUIRY. By W. G. AITCHISON ROBERTSON, M.D. (Edin.), D.Sc., F.R.S.E.

THE following investigation was pursued in furtherance of previous studies in the same field. It has reference chiefly to the normal physiological processes which take place in starch proteolysis, as induced by the ferment of ordinary mixed human saliva.

The effect of ptyalin on starch alone has been for long well known. Hitherto, however, no extensive series of observations have been made on amylolysis by ptyalin in mixed diets. To determine the question whether the digestion of starch is affected favourably or unfavourably by its admixture with other articles of food, seems to me to be of immense importance as regards the selection of a proper diet for invalids and infants.

To know which is the most easily digested form of bread; whether it is more easily digested when taken alone or along with some other article of food or drink; in what forms potatoes, rice, etc., are most digestible, and other like questions, appear to be dietetic problems of the utmost importance.

It is of interest to remember that the largest proportion of proteid matter which we consume is of vegetable origin. We are thus compelled to eat a large amount of carbohydrate material along with the proteid.

The following table shows how little proteid matter is present in flesh; and consequently the smallness of the amount of nitrogenous matter which we obtain in consuming the ordinary quantity of flesh is evident.

Composition of Flesh.

	Ox.	Fowl.
Water,	77·50	77·30
Solids,	22·50	22·7
Soluble albumin,	2·20	3·
Insoluble albumin,	17·50	16·5
Fat, etc.,	2·30	3·2

It is a common observation that starchy matters are frequently badly digested by certain individuals. In the treatment of this, which is termed 'amylaceous dyspepsia,' many forms of diastase are employed as digestive agents, viz.—malt, maltine, malt extracts, taka-diastase, etc. Those, it is said, convert, much more energetically than ptyalin, starchy matters present in the stomach. Even if this is so (and it is extremely doubtful whether many of the forms of malt extract have any diastatic action on starch), it is certainly most undesirable to have large quantities of sugar produced at once in the debilitated stomach. By such means it is not unlikely that we disturb the equilibrium of digestion and absorption, and render the advent of fermentative changes easy. If, on the other hand, as happens normally in nature, the starch is less rapidly converted, the sugar thus produced is absorbed slowly into the portal circulation. The artificially separated diastase of malt to a very large extent converts starch into dextrins and maltose, and hardly any into glucose. Such a proceeding is not a normal physiological result, and we could hardly imagine that the salivary ferment would have much effect on such products.

At best, however, these agents separated from malt form poor substitutes for those produced in the body during the act of digestion, and which doubtless vary their composition according to the requirements of the ingested material.

Besides this, it is well known that malt has a retarding influence on proteid digestion. Thus, in partaking of a mixed diet, what we might gain in rapidity of starch conversion through the agency of malt diastase (a doubtful advantage), we lose in the delay of proteid digestion.

In many cases, also, where such preparations of malt are given, not on account of their digestive action, but as foods in constitutional debility, etc., they give rise to acidity, nausea, with

very frequently persistent and troublesome itching of the skin. On leaving off these malt preparations, these symptoms soon disappear.

Instead of this (in many cases) experimental use of an artificial digestant for starch, it is surely far better to study the precise action of the salivary ferment itself on starchy foods in their simplest form, as well as in more complex combinations. In this way an exact dietary could be drawn out for each case of 'amylaceous dyspepsia.'

In other papers I have very fully entered into the question of the digestion of starch during its stay in the stomach and intestines: I therefore pass by this subject of the digestion of starch by the gastric juice entirely, merely stating that the amount of starch which undergoes conversion by the normal acidity of the gastric juice must be exceedingly limited, and that the gastric juice can be in no way considered as a digesting agent for starch.

Secretion of Saliva.—This is said to amount to from 200 to 1500 grammes per twenty-four hours. Bidder and Schmidt, however, put the minimum at 1000 grammes, and the maximum at 2000.

I have investigated this in my own case, and the following are averages got from many observations.

Method of investigation.—I carefully weighed the quantity of food which I would have eaten at the various meals, and then proceeded to masticate it. Instead of swallowing it, however, it was put out, and when all had been masticated, again carefully weighed. The increase in weight, of course, corresponded to the amount of saliva added during the process of mastication.

During the intervals between meals the saliva which would naturally have been swallowed was carefully collected and measured.

No two days give corresponding results; and this is easily accounted for, because different foods stimulate to a greater or less degree salivary secretion: not only so, but different occupations affect it,—manual labour or outdoor exercise lessening the secretion, while sedentary occupations increase it. The varying mental conditions also markedly modify the amount secreted.

Breakfast.—Supping 6 oz. of porridge along with milk leads

only to a small salivary secretion, not amounting to more than 3 or 4 grammes. The porridge is quickly swallowed, and thus little opportunity is given for a larger admixture of saliva.

After eating the porridge, bread, butter, and cold meat to the amount of $5\frac{1}{4}$ oz. (=148·8 grammes) were chewed. After mastication it was again weighed, and showed that on an average 46·5 to 50 grammes saliva had been secreted.

Between breakfast and dinner (taken at 1·30 P.M.), the amount of saliva secreted during four and a half hours amounted to from 50 to 60 cubic centimetres.

Dinner.—As happened with porridge, little saliva is added during the supping of soup. During the mastication of $7\frac{1}{2}$ ounces of meat, potatoes and rice, 10 to 15 grammes saliva were added; a similar amount was added during the mastication of 5 ounces of milk pudding.

Between dinner and tea less saliva was secreted than between breakfast and dinner, and the amount seldom rose above 50 grammes.

Tea.—The process of masticating bread and butter along with tea produces a copious secretion of saliva. When $2\frac{3}{4}$ ounces of such bread and butter (toast) were masticated, from 47 to 53 grammes saliva were added,—very much the same as at breakfast.

Between tea and supper—sitting reading or writing—from 60 to 70 grammes of saliva were secreted.

Supper.— $2\frac{1}{4}$ ounces of plain bread and butter (=63·78 grammes) and 5 grammes cheese, when masticated, led to a production of from 40 to 45 grammes of saliva.

Between supper and bedtime (9–11.15 P.M.), from 30 to 40 grammes were secreted.

The *total amount* secreted was therefore, on an average, in my own case, as follows:—

Breakfast,	49·5	to	54 grammes.
Interval,	50	„	60 „
Dinner,	20	„	30 „
Interval,	35	„	55 „
Tea,	47	„	53 „
Interval,	60	„	70 „
Supper,	40	„	45 „
Interval,	30	„	40 „
	<hr/>		<hr/>
	331·5		407

Making all allowances for any loss, we find, therefore, that the amount of saliva secreted per twenty-four hours, in my own case, seldom exceeded 400 grammes.

To show how much saliva is secreted and unconsciously swallowed, I made the following observations on myself.

The salivary secretion was collected and measured during half an hour's reading after partaking of breakfast (of porridge, milk, tea, and fish), and it amounted to 35 grammes. On other occasions it varied slightly, but never fell below 30 grammes.

The amount collected after dinner is not nearly so copious, amounting to from 35 to 55 grammes in two and a half to three hours.

After tea, on the contrary, the secretion is much more copious, varying from 45 to 55 grammes per hour.

After supper (cocoa, toast, biscuit) the salivary secretion was also copious, and varied from 30 to 40 grammes per hour in many cases.

Agents which stimulate Salivary Secretion.

Hot water.—I have found that rinsing out the mouth with tepid water greatly promotes the flow of saliva. Within certain limits, the warmer the food or drink which we consume, the greater is the flow of saliva. The effect of this, as regards the physiological digestion of starch in the stomach, is, of course, apparent. We cannot swallow liquids which are too hot; and as starch proteolysis is most effective at a temperature of 38° C., it is readily seen how rapidly and extensively starch must be converted when the amount of ptyalin is increased.¹ Thus, though tea be a great hindrance to starch proteolysis, from the presence of tannin, yet, from the copious flow of saliva which it induces, we rarely meet with amylaceous dyspepsia as a result of its use.

¹ As an objection to this, it may be said that in those cases of copious salivary secretion, it is only the watery constituent which is increased, the ferment, ptyalin, being in very small amount. As a result of many experiments on the amylolytic power of saliva collected as a result of stimulation by different forms of food and drugs, I cannot find that the amount of ptyalin is at any time diminished to any appreciable extent either in quantity or amylolytic power. The details of these experiments cannot, however, be given here.

Alcohol.—In the form of brandy or whisky, alcohol forms a powerful stimulating agent in promoting the flow of saliva. Even in weak dilution, it acts energetically; but the stronger the alcohol, the more powerful it is as a sialogogue.

Wines.—Contrary to expectation, these do not promote the flow of saliva; sherry produces a more abundant secretion of mucus.

Beer.—Bitter beer forms a powerful sialogogue.

Sugar.—In the form of sweets, this produces a copious flow of saliva. No doubt this is in part due to mechanical stimulation of the buccal mucous membrane. It is also, however, largely the result of stimulation of the sensory nerves of taste.

Mechanical irritation of the buccal mucous membrane by insoluble substances (*e.g.*, quill, pin, etc.) forms also a powerful sialogogue.

Employment.—During reading or writing the secretion is much more abundant than while performing any ordinary mechanical work or walking.

The following table (compiled from several sources) is of interest in showing the relative proportions of food elements present in the chief forms of carbohydrate food:—

	Water.	Albumin.	Carbohyd.	Fats.	Salts.
Wheaten flour, .	15	11	70·3	2	1·7
Oatmeal, . .	15	12·6	63	5·6	3
Barley, . . .	15	6·3	74·3	2·4	2
Rice,	12·4	7·4	79·4	0·4	0·4
Rye,	15	8	73·2	2	1·8
Maize,	13·5	10	64·5	6·7	1·4
Arrowroot, . .	16·5	0·8	82·4	...	0·19
Potatoes, . .	74	1·5	23·4	...	1·1
Bread (white), .	40	8	49·2	1·5	1·3
Biscuit, . . .	8	15·6	73·4	1·3	1·7
Peas,	12·3	26·7	56·4	1·7	2·9
Beans,	12·6	23·1	59·2	2	3·1
Tapioca, . . .	2	0·63	97·8	...	0·2
Macaroni, . . .	13·1	9	76·8	0·3	0·8
Sago,	12·8	0·81	86·1	...	0·19
Chocolate, . .	12	20	10	50	4
Apples (canned), .	83·2	0·2	15·9	0·4	0·3
Pears,	83	0·36	16·3	...	0·31
Bananas,	23·3
Turnips, . . .	85	2·95	6·9	0·2	1·2
Carrots, . . .	87·05	1·04	10·1	0·21	0·9
Cabbage, . . .	89·9	1·89	6·2	0·2	1·2
Melon,	2·5

As regards the richness of these in starch, the following is the order :—

	Per cent.
1. Tapioca,	97·8
2. Sago,	86·1
3. Arrowroot,	82·4
4. Rice,	79·4
5. Macaroni,	76·8
6. Barley,	74·3
7. Biscuit,	73·4
8. Rye,	73·2
9. Flour (wheat),	70·3

METHOD OF INVESTIGATION.

I investigated how far and in what kind of manner salivary digestion proceeded in the various starchy foods after they were cooked and prepared for the table.

Ten grammes of each of the various foods were accurately weighed out, placed in a large test-tube, heated to 38° C.; 2 cubic centimetres of mixed human saliva¹ (filtered to remove mucus) were added. A series of these tubes was prepared, and the whole was placed on a water-bath kept at a uniform temperature of 38° C. At frequent intervals the tubes were well shaken, so as to ensure thorough mixing of the starchy material with the saliva. At intervals of 5, 10, 20, 30, 45, 60, 90, 120, 150, 180 minutes a tube was removed, and the condition of its contents noted. The contents of the tube were then rapidly boiled, to prevent any further amylolytic action of the saliva. The sugar was then extracted by repeated washing with water and filtering. The filtrate was made up to a definite volume and the sugar estimated quantitatively as dextrose, so as to be comparable with the dextrose obtained by boiling the starchy material with dilute acid. Actually, maltose is the sugar produced in greatest amount as a result of salivary proteolysis, and it has a far feeblereffect in reducing Fehling's solution than has dextrose (the proportion being 65:100). For ease in comparison all the sugar produced has been calculated, however, as dextrose.

¹ The collection of saliva was always made in the evening, as Hofbauer has shown that there is great variation in the composition of saliva at different hours of the day (*Archiv für die gesammte Physiologie*, 1896-7, Bd. 65, p. 503-15).

I. *Ordinary Whole Rice.*

This was prepared in the ordinary way by boiling until quite soft. A watery extract showed that it consisted solely of unchanged starch, with practically no sugar. Ten grammes of this boiled rice were mixed with 2 c.c. saliva, kept at 38° C., and examined at intervals up to the end of three hours.

When 10 grammes of the rice were slowly masticated, the weight was increased to 11.16 grammes, showing an addition of 1.16 gramme saliva. This was examined at once, as also after being kept at 38° C. for thirty minutes.

When 10 grammes of this boiled rice were boiled for ten hours with dilute sulphuric acid, in order to convert the whole of the starch into glucose, it was found that 2.92 grammes of this sugar were present. We may therefore take this figure as the standard with which to compare the degree of salivary digestion during the various periods of exposure.

The results of these experiments are shown in the following table:—

TABLE I.—*Salivary Digestion of Cooked Rice—10 grammes.*

	Unchanged Starch.	Soluble Starch.	Erythro- dextrin.	Achroo- dextrin.	Dextrose. grammes.
Cold-water extract, . .	all	0	0	0	0
Converted wholly, . .	0	0	0	0	2.92
Masticated,	nearly all	little	trace	0	0.357
Masticated, then 30 min. at 38° C.,	„	much	fair amt.	little	0.361
2 cc. saliva at 38° C. 5 min.,	„	some	small amt.	0	0.156
„ „ 10 „	much	much	„	trace	0.156
„ „ 20 „	„	„	little	„	0.315
„ „ 30 „	„	still more	good amt.	more	0.322
„ „ 45 „	„	much	much	much	0.344
„ „ 60 „	„	not so much	still more	still more	0.393
„ „ 90 „	„	„	„	„	0.454
„ „ 120 „	not so much	still less	„	much	0.520

From this table it is evident that the action of mastication has, as one would have thought, caused a greater degree of conversion of the rice than when saliva acted on the whole rice. In the process of chewing, little more than 1 gramme of saliva

was added, whilst in the artificial digestion 2 grammes were added. The degree of subdivision of the grains has been in this case the cause of the hastened proteolysis.

After half an hour's exposure to the action of ptyalin in the test-tube, only about one-ninth of the rice starch has been changed completely into sugar: this is within the usual time during which the salivary ferment is active in the stomach. Of course, besides the sugar, soluble starch and dextrins have been produced likewise.

II. *Ordinary well-boiled Porridge.*

1. A cold-water extract shows it to consist of unchanged starch, with practically no sugar.

Ten grammes of porridge were mixed with 2 c.c. saliva, kept at 38°, and examined at varying intervals, as shown in the table.

When masticated slowly, 1·11 gramme saliva is added to each 10 grammes porridge.

Ten grammes porridge, boiled for ten hours with dilute sulphuric acid to convert all the starch, contains 1·03 grammes dextrose. (This is equal to 0·927 gramme starch which has undergone complete conversion.)

TABLE II.—*Salivary Digestion of Porridge—10 grammes.*

	Unchanged Starch.	Soluble Starch.	Erythro- dextrin.	Achroo- dextrin.	Dextrose, grammes.
Cold-water extract, . . .	all	0	0	0	0
Converted wholly, . . .	0	0	0	0	1·03
Masticated, . . .	nearly all	little	little	0	0·149
Masticated, then 30 min. at 38°, . . .	„	much	much	trace	0·265
2 c.c. saliva at 38° for 5 min.,	„	much	traces	0	0·115
„ „ 10 „	much	„	more	0	·128
„ „ 20 „	less	not so much	much	traces	·158
„ „ 30 „	some	little	„	much	·188
„ „ 45 „	„	„	„	„	·194
„ „ 60 „	„	„	„	„	·2
„ „ 90 „	little	„	more	more	·211
„ „ 120 „	very little	very little	„	„	·226

In this case, also, mastication has been productive of a larger amount of sugar from the starch than the artificial method. The amount of soluble starch begins to diminish after twenty minutes' digestion, and it is just at this period that the amount of dextrans increases greatly.

Before proceeding to investigate the effect which the addition of milk might have in influencing amyolysis, I made the following experiments with added water.

Does the degree of dilution of the starchy medium have any effect in hastening or retarding the proteolysis of starch ?

III. *Porridge with an equal volume of Water added, corresponding to thick Gruel.*

Ten grammes porridge—10 c.c. water—thoroughly mixed.

A cold-water extract shows only the presence of unchanged starch.

Two c.c. saliva were added to 10 c.c. water and 10 grammes porridge, placed at 38° C., and examined at intervals.

TABLE III.—*Salivary Digestion of Porridge with an equal volume of Water added—10 grms. of each.*

	Unchanged Starch.	Soluble Starch.	Eythro- dextrin.	Achroo- dextrin.	Dextrose. grammes.
Cold extract,	all	0	0	0	0
Totally converted, . . .	0	0	0	0	1·03
Masticated,	all	0	0	0	0·172
Masticated, and at 38° for 30 min.,	some	much	small amt.	0	0·308
2 c.c. saliva at 38° for 5 min.,	nearly all	"	"	0	0·153
" " 10 "	much	"	larger amt.	0	0·26
" " 20 "	"	"	still more	traces	0·263
" " 30 "	"	"	good amt.	"	0·294
" " 45 "	"	still more	"	"	0·303
" " 60 "	"	"	"	fair amt.	8·312
" " 90 "	little	"	still larger	"	0·335
" " 120 "	"	not so much	"	much	0·357

Evidently the dilution of the porridge has allowed the salivary ferment to act more readily on the starch contained in the oat-meal; for, in every case, the amount of sugar formed is greater

than when saliva acts on porridge alone. There is an increase in every case of about 0·12 gramme. Greater quantities of erythro- and achroo-dextrins are also formed in the dilute solution than in the case of porridge itself. With porridge alone the formation of soluble starch began to lessen after twenty minutes' exposure to the conversive ferment; while in the case of the watery porridge, soluble starch was formed up to the end of the first ninety minutes. The digestion of starch began more rapidly in the latter case also; for, after exposure to ptyalin for ten minutes, 0·26 gramme dextrose was formed, while with simple porridge only, 0·128 gramme was formed during this period. The after progress in the dilute solution, however, is not so marked as with porridge alone; for in the present case the amount of dextrose formed between the intervals of five and one hundred and twenty minutes is only 0·09 gramme, while during the same interval, in the porridge alone 0·109 gramme has been formed.

IV. *Porridge with equal volume Milk.*

Ten grammes porridge were thoroughly mixed with 10 c.c. fresh milk, heated to 38° C., and then 2 c.c. saliva added. The mixture was then kept at a uniform temperature of 38° C. for varying periods. At the expiry of these, the condition of the starch was investigated, and the fluid boiled to stop further amylolytic action. The casein was coagulated by adding one or two drops of acetic acid, and the sugar washed out by repeated washing with water on a filter.

The amount of milk-sugar normally present in 10 c.c. milk was carefully estimated, and deducted from the total amount of sugar found in each observation. The lactose present in each 10 c.c. of milk amounted to 0·406 gramme, or if calculated as dextrose, 0·303.

[TABLE IV.]

TABLE IV.—*Salivary Digestion of Porridge and Milk—
equal volumes.*

	Unchanged Starch.	Soluble Starch.	Erythro- dextrin.	Achroo- dextrin.	Dextrose. grammes.
Cold water,	all	0	0	0	0
Wholly converted, . . .	0	0	0	0	1·03
Masticated,	all	trace	0	0	0·021
Masticated, and at 38° for 30 min.,	much	much	fair amt.	0	0·247
2 c.c. saliva at 38° for 5 min.,	„	„	little	0	0·151
„ „ 10 „	„	„	good deal	trace	0·197
„ „ 20 „	„	little	much	much	0·247
„ „ 30 „	not so much	less	still more	still more	0·258
„ „ 45 „	„	very little	large amt.	large amt.	0·265
„ „ 60 „	„	traces	almost all	„	0·292
„ „ 90 „	„	„	„	„	0·322
„ „ 120 „	„	„	„	„	0·365

Dilution of the porridge with milk has in this case also furthered the action of the salivary ferment. Up to the expiry of ninety minutes, however, the amount of the complete conversion into sugar is not so great as with the simple dilution with water. With the porridge and milk the conversion of starch into dextrins is much more rapid than in the watered porridge. Before the lapse of twenty minutes, the formation of soluble starch decreases, while the higher dextrins are rapidly and increasingly produced.

Towards the end of the second hour, sugar begins to be formed much more rapidly than in the case of simple dilution with water.

If we compare this table with that of the digestion of porridge alone, we note that the addition of milk has favoured an increased degree of conversion of starch. In both, the amount of soluble starch begins to show a decrease after the twentieth minute.

Erythrodextrin, which up to this period has been much the same in both cases in point of quantity, now rapidly increases in the case of porridge + milk, and reaches a much higher amount than in the case of porridge alone. The same occurs with achroodextrin; and in the case of dextrose, even from the first five minutes there is an excess of 0·036 gramme over the porridge

alone. This excess gradually and steadily increases, until at the end of the second hour the porridge + milk has an advantage of 0.139 gramme dextrose over the simple porridge.

V. Salivary Digestion of Corn Flour.

The corn flour was boiled with water for eight minutes ; a firm, transparent jelly resulted.

TABLE V.—*Salivary Digestion of Corn Flour.*

	Unchanged Starch.	Soluble Starch.	Erythro-dextrin.	Achroo-dextrin.	Dextrose. grammes.
Cold extract,	all	0	0	0	0
Wholly converted, . . .	0	0	0	0	0.902
Masticated,	much	much	very little	0	0.25
Masticated, and at 38° for 30 min.,	trace	„	much	trace	0.344
2 c.c. saliva at 38° for 5 min.,	much	some	0	0	0.25
„ „ 10 „	„	much	little	0	0.256
„ „ 20 „	„	„	„	trace	0.263
„ „ 30 „	„	„	much	more	0.277
„ „ 45 „	less	„	still more	„	0.290
„ „ 60 „	„	„	„	„	0.310
„ „ 90 „	„	„	„	much	0.33
„ „ 120 „	still less	„	„	„	0.378
„ „ 150 „	small amt.	less	large amt.	large amt.	0.384
„ „ 180 „	trace	very little	„	„	0.406

At the end of three hours' artificial digestion not one-half of the available starch has undergone complete conversion into sugar, though at this time what remains has been almost wholly converted into dextrans. The process of mastication has greatly hastened conversion, as after being masticated and kept at 38° C. for thirty minutes, more sugar was formed than was produced by ninety minutes' artificial digestion.

Corn flour undergoes a rapid and fairly complete digestion within even the first three-quarters of an hour ; and were it diluted further with water or milk, the rate and degree of conversion would be increased.

VI. Salivary Digestion of Boiled and Powdered Potatoes.

The potatoes were boiled, then forced through a potato-masher having fine holes. They were thus brought into a much

finer state of subdivision than is usual even after the mastication of a potato. In this way the saliva had ready access to the starch.

TABLE VI.—*Salivary Digestion of Boiled and Powdered Potato—
10 grammes.*

	Unchanged Starch.	Soluble Starch.	Erythro- dextrin.!	Achroo- dextrin.	Dextrose. grammes.
Cold-water extract, . .	all	0	0	0	0·03
Wholly converted, . .	0	0	0	0	3·04
Masticated, . .	much	fair amt.	0	0	0·520
Masticated, and at 38° for 30 min., . .	little	0	0	much	0·617
2 c.c. saliva at 38° for 5 min.,	much	fair amt.	fair amt.	0	0·423
„ „ 10 „	„	much	very much	much	0·427
„ „ 20 „	some	„	much	„	0·657
„ „ 30 „	„	small amt.	„	„	0·657
„ „ 45 „	„	„	small amt.	„	0·757
„ „ 60 „	„	very little	very little	good amt.	0·757
„ „ 90 „	little	trace	trace	fair amt.	0·833
„ „ 120 „	„	„	„	„	0·877
„ „ 150 „	very little	merest tr.	none	„	0·892
„ „ 180 „	„	„	„	„	0·892

At the expiry of three hours' artificial digestion, a little more than one-quarter of the starch normally present in cooked potato has been wholly changed into sugar. In the case of potato, the process of mastication has had a little advantage over simple digestion on the water-bath; but, as prepared, the potato was finely powdered, and so freely acted upon by the added saliva. No more intimate mixing could be produced by chewing. That the starch of the potato thus prepared is easily and rapidly acted upon by the saliva, is shown by the fact that after having been simply masticated, a fair amount is rendered soluble, and 0·520 gramme, or more than one-sixth of the total starch, changed into sugar.

The limit of possible conversion in this experiment seems to have been reached in from two to two and a half hours. After this period no further change has taken place either in the amount of sugar formed or in the condition of the starch or dextrins.

VII. *Salivary Digestion of Boiled Potatoes merely broken into fragments, to represent what might happen during mastication.*

TABLE VII.—*Salivary Digestion of Boiled Potato (in fragments).*

	Unchanged Starch.	Soluble Starch.	Erythro-dextrin.	Achroo-dextrin.	Dextrose. grammes.
Cold-water extract, . . .	all	0	0	0	0
Wholly converted, . . .	0	0	0	0	3·04
Masticated, . . .	much	much	faint trace	0	0·298
Masticated, and at 38° for 30 min., . . .	0	0	0	much	0·657
2 c.c. saliva at 38° for 5 min., . . .	much	much	present	0	0·277
„ „ 10 „ . . .	„	„	little	trace	0·45
„ „ 20 „ . . .	„	„	„	„	0·454
„ „ 30 „ . . .	„	„	much	much	0·460
„ „ 45 „ . . .	„	„	„	„	0·494
„ „ 60 „ . . .	only in lumps	0	„	„	0·476
„ „ 90 „ . . .	„	0	„	„	0·520
„ „ 120 „ . . .	„	0	„	„	0·543
„ „ 150 „ . . .	„	„	„	„	0·55
„ „ 180 „ . . .	„	„	„	„	0·561

In this set of experiments we find the iodine starch reaction soon giving negative results. That is to say, that the saliva has acted on the smaller particles, and has converted them wholly into achroodextrin and sugar. The same had occurred on the surface of the larger masses, but the saliva has been unable to penetrate the larger pieces and convert the starch inside them. Thus we have at an early period all the easily accessible starch changed into achroodextrin and sugar.

Looking over the column showing the amounts of sugar produced by the artificial digestion by saliva, we note that the figures are not perfectly progressive with the length of time digested. This irregularity is easily explained, however. The size of the potato fragments was by no means uniform in the different test-tubes. The larger fragments were consequently less acted on than the smaller, as they presented a relatively smaller surface to the digestive fluid. Thus the amount of sugar produced was less in some tubes than in others. On the whole, however, we note a steady enough increase in the amount of sugar produced.

It is more interesting to compare this table with the preceding. We notice that the amount of starch converted in the present set of experiments is much less than it was in the preceding set. Thus, after twenty minutes' heating, the powdered potato has produced 0.657 gramme sugar, while the potato in fragments has only produced 0.454 gramme. At the end of the third hour the figures are 0.892 against 0.561 gramme. In the case of powdered potato the starch has almost entirely disappeared, while in the present case it is yet unconverted in the interior of the larger fragments.

This shows how very important the mode of preparation of such an article of food as potato is. There can be no doubt but that the fineness of division of the potato hastens its digestion. Nor is it practically possible to masticate an ordinary potato sufficiently to render it as digestible as it is when powdered artificially. In proof of this, we find that the chewed whole potato when examined at once possessed only 0.298 gramme sugar, while the chewed but previously powdered potato had 0.520 gramme. We see that, after having been kept at 38° C. for thirty minutes, the ordinary masticated potato possesses 0.657 gramme sugar in contrast with 0.617 gramme sugar in the powdered potato treated in the same way. This apparent contradiction is, however, explained by the fact that I purposely chewed the ordinary whole potato more thoroughly, and for a long time, in order to observe how much sugar could be produced by the admixture with saliva during simple mastication.

Even at the end of three hours we cannot say that the potato (in fragments merely) has been digested. The smaller fragments have, however, been dissolved, but the larger ones have only had their surface acted on by the amylolytic ferment. This, then, is a good example for the beneficial results which follow from a proper preparation of food for the table.

VIII. *Salivary Digestion of Bread.*

This was ordinary plain bread without the crust, the second day after baking, and crumbled into small fragments.

Ten grammes of this formed too bulky a quantity to deal with. I therefore used 5 grammes only, and to this 2 c.c. saliva were

added. Even with this reduction, the bread is really only moistened at one spot, and at the end of three hours' heating at 38° C., a large part was quite dry and unacted upon, while the fragments which were moistened had become quite pulpy. The results of this series of experiments are consequently so irregular that I need not detail them, merely stating that the irregularity was due to the unequal and localised action of the saliva on the bread crumb.

1. When 5 grammes bread are thoroughly well chewed, the weight increases to 7.74 grammes, showing that 2.74 grammes saliva have been secreted during the process. The bread then shows the presence of much unchanged starch, along with some soluble starch and erythrodextrin, while 0.26 gramme sugar is present.

2. When 5 grammes bread are chewed thoroughly, and then kept at 38° C. for thirty minutes, the sugar increases to 0.854 gramme, and while much unchanged starch is yet present, soluble starch and erythrodextrin are present in much larger amounts.

3. A cold watery extract of 5 grammes bread shows that only unchanged starch is present, along with a very small amount of soluble starch, and sugar amounts to 0.042 gramme.

TABLE VIII.—*Ordinary White Bread—5 grm. + 2 c.c. saliva.*

	Unchanged Starch.	Soluble Starch.	Erythro- dextrin.	Dextrose. grammes.
Cold-water extract, . . .	nearly all	little	?	0.042
Masticated, . . .	much	some	little	0.26
Masticated, and at 38° C. for 30 min., . . .	much	much	much	0.854
Totally converted, . . .	0	0	0	2.174

This shows that more than one-fifth of a gramme of starch has been converted by simply chewing the bread. I must, however, again draw attention to the fact that the mastication was most complete and deliberate, and not the incomplete operation which it usually is. If it be kept at the body temperature for half an hour after being well masticated, about two-fifths of the whole undergo conversion into sugar.

It is, however, a very unusual occurrence to eat dry bread alone. It is nearly always accompanied by some fluid or beverage. As the simplest, I experimented with water in the first instance.

IX. Salivary Digestion of Bread Crumb with Water.

Ten c.c. of water (previously heated to 38° C.) were mixed with 2 c.c. of ordinary mixed saliva and poured over 5 grammes bread crumb (also at temperature of 38° C.). This amount of fluid moistened the bread thoroughly.

TABLE IX.—*Salivary Digestion of Bread (5 grms.) along with Water (10 c.c.).*

Cold-water extract, . . .	nearly all	little	?	0	0.042
Totally converted, . . .	0	0	0	0	2.174
Masticated, + 10 c.c. water, .	much	much	present	?	0.505
Masticated, and at 38° for 30 min.,	little	„	much	much	0.706
2 c.c. saliva at 38° for 5 min.,	much	present	trace	?	0.289
„ „ 10 „	much	much	trace	?	0.311
„ „ 20 „	„	„	present	?	0.476
„ „ 30 „	„	„	good amt.	present	0.574
„ „ 45 „	„	„	more	„	0.639
„ „ 60 „	decreasing	very much	large amt.	„	0.704
„ „ 90 „	present	„	„	„	0.726
„ „ 120 „	„	„	„	„	0.746
„ „ 150 „	„	„	„	large amt.	0.769
„ „ 180 „	little	„	very „ „	very „ „	0.849

As preceding examples have demonstrated, so does this experiment, that a proper dilution greatly hastens salivary proteolysis. In the case of bread chewed alone, only 0.26 gramme dextrose resulted; while when chewed with 10 c.c. water, 0.505 grammes are produced, or almost exactly double the amount. Evidently the dilution and general moistening of the bread produces a marked rapidity in the action of ptyalin, for after having been chewed and kept at 38° C. for thirty minutes, the dilute saliva has produced 0.706 gramme, while during the same period the bread chewed alone showed that the pure saliva had produced 0.854 gramme dextrose. This is to say, that the dilute

saliva acted more rapidly on the starch of the bread, but that its ultimate effect was feeble than that of the pure saliva when allowed to act for a certain time. Though dilution hastens amylolysis, yet it would seem that the process does not go so far in the production of sugar as when pure saliva acts on the starch of bread; for example, at the end of three hours' artificial digestion, 0·849 gramme sugar has been produced in the dilute solution, while 1·33 grammes dextrose (or more than one-half of the total starch present) were produced by the action of 2 c.c. saliva on 5 grammes bread alone. In the dilute saliva, however, very little unchanged starch remains at the end of three hours, for nearly all has been converted into soluble starch or dextrans.

It is well known that newly-baked bread is indigestible. Is this shown in its action to the salivary ferment?

X. Salivary Digestion of Newly-baked Bread Crumb.

Five grammes newly-baked bread crumb; 10 c.c. water and 2 c.c. saliva; at 38° C.

TABLE X.—*Salivary Digestion of Newly-baked Bread along with 10 c.c. Water.*

	Unchanged Starch.	Soluble Starch.	Erythro-dextrin.	Achroo-dextrin.	Dextrose. grammes.
Cold-water extract, . . .	nearly all	little	?	?	0·042
Wholly converted, . . .	0	0	0	0	2·174
Masticated, . . .	much	present	present	0	0·384
Masticated, and at 38° C. for 30 min.,	much	much	much	present	0·742
2 c.c. saliva at 38° for 5 min.,	„	present	mere trace	0	0·384
„ „ 10 „	„	fair amt.	little	0	0·510
„ „ 20 „	much	much	little	?	0·537
„ „ 30 „	„	„	„	trace	0·568
„ „ 45 „	„	„	fair amt.	present	0·704
„ „ 60 „	„	„	good amt.	„	0·735
„ „ 90 „	not so much	„	much	„	0·83
„ „ 120 „	„	„	„	„	0·851
„ „ 150 „	„	„	„	much	0·857
„ „ 180 „	still less	not so much	very large amount	very large amount	0·927

Did we look merely at the result of chewing on this freshly-baked bread (examined immediately) we would say that cer-

tainly it was less easily digested than stale bread; for only 0.384 gramme dextrose results in the one case, as compared with 0.505 gramme in the other. This is, however, not borne out by a further consideration of the process of salivary digestion. In fact, all through we find that the newly-baked bread has undergone a more rapid and extensive change than the staler bread. In the freshly-baked bread the starch granules will still be in a moist condition, and so more readily acted upon by the saliva than in the second day's bread, which has undergone a partial drying, so rendering the starch granules less easy of amylolysis.

We can easily account for the apparent difficulty in reconciling the fact that less sugar is produced by chewing the fresh bread than by chewing the old. When we try to crumble freshly-baked bread it will hardly do so, but becomes sodden and doughy. The same results appear during the process of mastication. Thus the saliva acts less rapidly on this doughy mass than on the separate crumbs of stale bread. This sodden condition does not persist long when the bread is exposed to moisture. It soon swells up and starch digestion proceeds rapidly, as is shown by the fact that when chewed and exposed to the action of saliva for 30 minutes, 0.742 gramme sugar is produced from the newly-baked bread, as compared with 0.706 gramme from the stale bread.

The bread crumb of newly-baked bread, though more compact than that of stale bread, rapidly absorbs the fluid, and swelling up, the still moist starch granules become easily acted upon by the proteolytic ferment. In this way we have a rapid and extensive change of starch.

It therefore does not appear as a result of these experiments that newly-baked bread is less easily digested than stale bread. They rather prove the reverse, so far as salivary digestion alone is concerned.

XI. Salivary Digestion of the Outside Crust of Stale Bread.

The crust of bread is popularly believed to be more nutritious and easily digested than the crumb, as the starch has undergone dextrinisation through the heat? Is this borne out in its behaviour to the salivary ferment?

TABLE XI.—*Salivary Digestion of Crust of Bread—5 grammes crust, 10 cc. water, 2 cc. saliva.*

	Unchanged Starch.	Soluble Starch.	Erythro-dextrin.	Achroo-dextrin.	Sugar. grammes.
Cold-water extract, . . .	much	much	trace	...	0·066
Wholly converted, . . .	0	0	0	0	3·03
Masticated, . . .	much	much	trace	...	0·744
Masticated, and at 38° for 30 min.,	„	„	fair amount	?	1·0
2 cc. saliva at 38° for 5 min.,	„	„	good amt.	trace	0·267
„ „ 10 „	„	„	„	„	0·275
„ „ 20 „	„	„	much	present	0·316
„ „ 30 „	„	„	„	fair amt.	0·474
„ „ 45 „	„	„	„	„	0·5
„ „ 60 „	„	less	„	„	0·542
„ „ 90 „	less	little	„	much	0·588
„ „ 120 „	present	„	not so much	„	0·649
„ „ 150 „	„	very little	less	„	0·681
„ „ 180 „	„	„	trace	„	0·713

These products of digestion filtered with extreme difficulty, owing to the amount of gummy dextrin present.

The crust of bread does contain a large amount of dextrin, but it does not seem to undergo much higher conversion under the influence of ptyalin. After three hours' artificial digestion not one-quarter of the available sugar has been formed from starch in the case of crust; while, in the same period, with newly-baked bread almost one-half of the available sugar was formed from starch. During the process of digestion soluble starch and erythrodextrin have been converted into achroo-dextrin to a large extent, but little of the latter becomes changed into reducing sugar. On account of the presence of so much soluble starch and dextrans and to their easy transformation into higher varieties, the crust of bread is thus perhaps more easily assimilated than ordinary bread crumb.

Does the structure of bread modify its reaction to the salivary ferment? That is to say, if the bread is lighter in consistence or more porous, is it more easily digested?

In order to determine this, I took a very spongy variety of bread, known as Vienna bread, and subjected it to the same set of experiments as had previously been carried out with

ordinary stale bread. It is not usual to eat this bread stale, but for purposes of comparison it was tried.

XII. Salivary Digestion of Stale Vienna Bread—5 grammes bread, 10 cc. water, 2 cc. saliva, at 38° C.

TABLE XII.—*Salivary Digestion of Stale Vienna Bread compared with stale ordinary bread in respect to amount of Sugar formed.*

	Un- changed Starch.	Soluble Starch.	Erythro- dextrin.	Achroo- dextrin.	Sugar. grammes	Stale Ordinary Bread. Sugar.
Masticated,	much	much	much	fair amt.	0·595	0·505
Masticated, and at 38° for 30 min.,	„	„	„	much	0·764	0·706
2 cc. saliva in . . . 5 min.,	„	„	fair amt.	present	0·55	0·289
„ „ 10 „	„	„	much	„	0·572	8·382
„ „ 30 „	„	„	„	„	0·595	0·574
„ „ 60 „	„	„	„	„	0·73	0·704
„ „ 120 „	„	„	„	much	0·781	0·746
„ „ 180 „	„	„	„	„	0·835	0·849

Before making any remark, I will give the results of experiments with new, freshly-baked Vienna bread. This is very light in texture, and even when chewed does not become sodden like ordinary bread.

XIII. Salivary Digestion of New Vienna Bread—5 grammes bread, 10 cc. water, 2 cc. saliva, at 38° C.

New Vienna Bread.—As was to be expected, there was a greatly increased degree of conversion in the case of this spongy bread. This is shown both as a result of chewing and also of simple artificial digestion by ptyalin. We note, however, that this increased degree of conversion persists only during the first two hours. At the end of the second hour more sugar has been formed from the ordinary bread than from the Vienna, and this goes on increasing during the third hour.

TABLE XIII.—*Salivary Digestion of New Vienna Bread compared with stale ordinary bread in respect of amount of Sugar formed.*

	Un- changed Starch.	Soluble Starch.	Erythro- dextrin.	Achroo- dextrin.	Sugar. grms.	Ordinary New Bread. Sugar.
Masticated, .	much	much	fair amt.	...	0·70	0·384
Masticated, and at 38° for 30 min.,	„	„	much	much	0·847	0·742
2 c.c. saliva at 38° for 5 min.,	„	„	some	?	0·455	0·384
„ „ 10 „	„	„	„	?	0·579	0·510
„ „ 80 „	„	„	much	much	0·704	0·568
„ „ 60 „	„	„	„	„	0·746	0·735
„ „ 120 „	„	„	„	„	0·770	0·851
„ „ 180 „	„	„	„	„	0·838	0·927

Stale Vienna Bread.—The results in this case are very similar to those found in the new Vienna bread, excepting that it is not until the end of the third hour that the ordinary bread (stale) gains on the porous bread in respect to the amount of sugar produced.

The lightness of the bread, therefore, is only of use in increasing the rapidity of starch conversion, and not in helping to increase the total amount of sugar formed.

What effect, if any, have some of the usual concomitants of bread, as butter or cheese, on amylolysis of starch by ptyalin? This seemed an interesting question to solve. I therefore give the results of these experiments.

XIV. *Salivary Digestion of Bread and Butter.*

Three grammes of salt butter were thoroughly mixed with five grammes of stale bread crumb; 10 c.c. water + 2 c.c. saliva were added, and all was kept at 38° C.

TABLE XIV.—*Salivary Digestion of Bread and Butter—5 grms. bread, 3 grms. butter, 10 c.c. water.*

	Un- changed Starch.	Soluble Starch.	Erythro- dextrin.	Achroo- dextrin.	Sugar. grms.	Bread and Water alone.
Watery extract,	nearly all	little	0	0	0·042	
Totally converted, . . .	0	0	0	0	2·174	
Masticated,	much	much	some	?	0·428	0·505
Masticated, and at 38° for 30 min.,	„	„	much	much	0·68	0·706
2 c.c. saliva at 38° for 60 min.,	„	„	?	0	0·694	0·704
„ „ 120 „	„	„	fair amt.	present	0·724	0·769
„ „ 180 „	„	„	„	„	0·845	0·849

There is a close parallelism between the results of this experiment and those obtained from plain bread and water. Butter is not at all a stimulus to salivary secretion, and so the amount of starch conversion is even less in the case of bread and butter than it is in the case of plain bread and water.

The addition of butter, therefore, to bread has little or no effect on amylolysis by ptyalin.

XV. *Salivary Digestion of Bread and Cheese.*

Four grammes of ordinary cheese in small fragments were mixed with 5 grammes of stale bread crumb and 10 c.c. water, together with 2 c.c. saliva, and kept at 38° C.

TABLE XV.—*Salivary Digestion of Bread and Cheese—cheese 4 grms., bread 5 grms., water 10 c.c.*

	Un- changed Starch.	Soluble Starch.	Erythro- dextrin.	Achroo- dextrin.	Sugar. grms.	Bread and Water alone.
Cold-water extract, . . .	nearly all	little	0	0	0·042	
Wholly converted, . . .	0	0	0	0	2·174	
Masticated,	much	much	some	some	0·755	0·505
Masticated, and at 38° for 30 min.,	„	„	much	much	0·808	0·706
2 c.c. saliva at 38° for 60 min.,	„	„	some	?	0·644	0·704
„ „ 150 „	„	„	fair amt.	some	0·737	0·769
„ „ 180 „	„	„	much	much	0·83	0·849

As regards artificial digestion, the addition of cheese seems to have had little or no effect on salivary amylolysis. If we had expected a more rapid conversion of starch as a result of chewing, we have not been disappointed. The cheese has caused an increased flow of saliva, and as a result an increased conversion of starch. Apart, therefore, from the consideration of its digestibility, cheese has a helpful action in promoting starch proteolysis, owing to its directly stimulating effect on the salivary glands.

Effect of Fluid Foods on Digestion of Starch by Saliva.

In order to investigate this I took as examples of very common foods milk and broth, and noted the reaction of the starch to ptyalin when either of these was added.

XVI. Salivary Digestion of Bread and Milk.

Five grammes of stale bread crumb were added to 10 c.c. fresh milk together with 2 c.c. saliva. This was kept at 38° C.

TABLE XVI.—*Salivary Digestion of Bread and Milk—5 grms. bread, 10 c.c. milk, 2 c.c. saliva.*

	Un- changed Starch.	Soluble Starch.	Erythro- dextrin.	Achroo- dextrin.	Sugar. grms.	Bread and Water. Sugar.
Masticated, .	much	much	some	?	0·152	0·505
Masticated, and at 38° for 30 min., .	„	„	much	some	0·621	0·706
2 c.c. saliva at 38° for 5 min.,	nearly all	some	traces	0	0	0·289
„ „ 10 „	much	more	more	?	0·083	0·382
„ „ 30 „	„	much	fair amt.	„	0·197	0·574
„ „ 60 „	„	„	„	„	0·492	0·704
„ „ 120 „	„	„	„	„	0·551	0·746
„ „ 180 „	„	„	„	„	0·671	0·849

In arriving at the above estimations of sugar, the amount of lactose present in 10 c.c. milk was first determined, and this amount was subtracted from the subsequent estimations.

The addition of milk to bread causes a remarkable enfeeblement of the salivary ferment. During practically the first twenty minutes no conversion of starch takes place. After this

period, however, the change goes on fairly rapidly, though it never by any means attains to that produced when water alone is taken along with bread.

Milk has therefore a retarding effect on the salivary ferment, and at the same time lessens its converting power.

XVII. *Salivary Digestion of Broth and Bread.*

Amongst our working-class population this is a very common (very often the sole midday) article of diet. It consequently seemed an interesting experiment to investigate in what manner the addition of broth might affect the digestion of starch by ptyalin.

The broth was made of meat and rice, but only the clear fluid was used in the experiments.

Ten c.c. of broth fluid along with 2 c.c. saliva were poured over 5 grammes stale bread crumbs. This was kept at 38° C.

TABLE XVII.—*Salivary Digestion of Bread and Broth—5 grms. stale bread, 10 c.c. broth fluid, 2 c.c. saliva.*

	Un- changed Starch.	Soluble Starch.	Erythro- dextrin.	Achroo- dextrin.	Sugar. grms.	Bread and Water Plain.	Differ- ence.
Masticated, . . .	much	much	much	present	0·467	0·505	·038
Masticated, and at 38° for 30 min., . .	„	„	„	„	0·73	0·706	·024
2 c.c. saliva at 38° for 5 min.,	„	„	some	?	0·320	0·289	·031
„ 10 „	„	„	„	„	0·323	0·382	·061
„ 30 „	„	„	good deal	„	0·542	0·574	·032
„ 60 „	„	„	„	„	0·698	0·704	·006
„ 120 „	„	„	much	„	0·769	0·746	—·023
„ 180 „	„	„	„	present	0·802	0·849	·047

Throughout this series of experiments (with one exception) the degree of starch conversion is less than in the case of bread and water alone. Evidently, either the saline or proteid matters present in the broth have had a slight restraining influence on the salivary ferment.

The retarding influence is, however, very slight as compared with that caused by milk.

XVIII. Salivary Digestion of Bread and Tea.

As we have seen, bread is seldom eaten alone. It is usually eaten along with some fluid, none being more used than tea infusion.

What effect on the salivary digestion of bread has an infusion of tea ?

The tea used was an ordinary good household tea, with a slight addition of Pekoe as flavouring. It was infused for ten minutes, and the infusion had an acidity equal to 0·86 per cent. tannic acid.

Ten c.c. of this infusion at 38° C. were mixed with 2 c.c. saliva and poured over 5 grammes stale bread crumb (2nd day).

We have to compare this table with that showing the digestion of bread along with water (Table IX.).

These experiments show that an infusion of tea hinders, though by no means inhibits, the action of ptyalin. Up to the end of the second hour, less sugar is formed from starch when in the presence of tea infusion than is formed in its absence. After this time-limit, however, no difference is noted either with or without tea infusion.

TABLE XVIII.—Salivary Digestion of Bread along with Tea—5 grms. bread, 10 c.c. tea infusion, 2 c.c. saliva.

	Un- changed Starch.	Soluble Starch.	Erythro- dextrin.	Achroo- dextrin.	Sugar. grms.	Bread and Water Plain.	Differ- ence.
Cold-water extract, Wholly converted by acid,	all	little	0·042		
Chewed, and at once examined,	0	0	0	0	2·174		
Chewed, and at 38° for 30 min.,	much	much	some	!	0·256	0·505	·249
2 c.c. saliva at 38° for 5 min.,	little	much	much	present	0·5	0·706	·206
„ 10 „	much	much	trace	!	0·161	0·289	·128
„ 20 „	„	„	present	present	0·273	0·382	·109
„ 30 „	„	„	fair amt.	„	0·359	0·476	·117
„ 45 „	„	„	„	„	0·412	0·574	·162
„ 60 „	„	„	„	„	0·596	0·639	·043
„ 90 „	„	„	much	more	0·602	0·704	·102
„ 120 „	not so much	not so much	grt. amt.	grt.amt.	0·653	0·726	·073
„ 150 „	„	„	„	„	0·714	0·746	·032
„ 180 „	„	„	„	„	0·769	0·769	
	little	little	„	„	0·845	0·849	·004

When bread is chewed along with tea infusion, only about one-half the amount of sugar is formed compared to the same proceeding with bread and water alone. After being chewed, if it be kept at 38° C. for half an hour, only half a gramme of sugar is formed, as compared with 0·706 gramme produced in the presence of water alone. During the early stages of digestion, therefore, there is a marked retardation produced by infusions of tea.

XIX. Salivary Digestion of Bread and Coffee.

Five grammes bread crumb were mixed with 10 c.c. ordinary decoction of coffee, along with 2 c.c. saliva, at 38° C.

TABLE XIX.—Salivary Digestion of Bread and Coffee—5 grms. bread, 10 c.c. coffee, 2 c.c. saliva.

	Un- changed Starch.	Soluble Starch.	Erythro- dextrin.	Achroo- dextrin.	Sugar. grms.	Bread and Plain Water.	Differ- ence.
Cold extract, . . .	nearly all	little	0	0	0·042		
Totally converted, .	0	0	0	0	2·174		
Chewed, and at once examined, . . .	much	lge. amt.	lge. amt.	0	0·36	0·505	0·145
Chewed, and at 38° for 30 min., . . .	„	„	„	„	0·637	0·706	0·069
2 c.c. saliva at 38° for 5 min., . . .	much	fair amt.	trace	0	0·268	0·289	·026
„ 10 „	much	much	fair amt.	?	0·348	0·382	·039
„ 20 „	„	„	„	„	0·485	0·476	·041
„ 30 „	„	„	much	„	0·531	0·574	·043
„ 45 „	„	„	„	„	0·570	0·639	·069
„ 60 „	„	„	„	„	0·670	0·704	·034
„ 90 „	„	„	„	„	0·719	0·726	·007
„ 120 „	„	„	„	„	0·722	0·746	·024
„ 150 „	„	„	„	„	0·750	0·769	·019
„ 180 „	„	„	„	„	0·753	0·849	·096

In the case of coffee, starch conversion commences early, and goes on steadily progressing. The maximum amount of sugar produced falls far short of that produced along with tea infusion. On comparing these tables it is well shown how strongly an inhibiting agent tea is. The figures in the “difference”

column are striking. We find, then, that coffee has no great effect in hindering or slowing starch proteolysis.

XX. *Salivary Digestion of Bread and Cocoa.*

Five grms. of bread crumb were mixed with 10 c.c. of cocoa solution and 2 c.c. saliva. The cocoa used was Van Houten's. An extract of this, made with boiling water, contains the merest traces of sugar, too small to be regarded, and when digested alone with 2 c.c. saliva for thirty minutes, no reaction with iodine is obtained, and no appreciable amount of sugar is formed.

The above mixture was kept at 38° C.

TABLE XX.—*Salivary Digestion of Bread and Cocoa.*

	Un- changed Starch.	Soluble Starch.	Erythro- dextrin.	Achroo- dextrin.	Sugar. grms.	Bread and Plain Water.	Differ- ence.
Cold-water extract, .	nearly all	little	0	0	0·042		
Totally converted, .	0	0	0	0	2·174		
Chewed, and at once examined, .	much	much	traces	traces	0·526	·505	·021 +
Chewed, and at 38° C. for 30 min., .	„	„	present	present	0·866	·706	·160 +
2 c.c. saliva at 38° 5 min.	„	„	„	0	0·281	·289	·008 –
„ 10 „	„	„	good amt	0	0·433	·382	·051 +
„ 20 „	„	„	much	!	0·590	·476	·114 +
„ 30 „	„	„	„	present	0·610	·574	·036 +
„ 45 „	„	„	„	„	0·630	·639	·009 –
„ 60 „	„	„	„	„	0·711	·704	·007 +
„ 90 „	„	„	„	„	0·756	·726	·030 +
„ 120 „	„	„	„	„	0·762	·746	·016 +
„ 150 „	„	„	„	much	0·788	·769	·019 +
„ 180 „	„	„	not so much	much	0·814	·849	·035 –

Naturally, we compare these results with those obtained in the case of tea and coffee. In the case of cocoa, we find there is little or no restraining action. Starch conversion begins early and proceeds steadily.

In the case of tea, conversion was at first restrained; later on, however, amyolysis proceeded more rapidly, until, at the end of two and a half hours, we find that the starch has undergone a greater conversion relatively to what we find in the case

of cocoa. Even from the first the starch undergoes solution almost as readily as it does when water alone is used.

Comparing cocoa with coffee, though the differences are not so marked as in the case of tea, yet the advantage rests with cocoa; there is less inhibition of ptyalin in the present case than in the case of coffee.

What effect have our ordinary stimulants on the salivary digestion of starch?

XXI. *Salivary Digestion of Bread along with Beer.*

Five grms. bread crumbs were mixed with 2 c.c. saliva and 10 c.c. Prestonpans beer (there is practically no sugar in 10 c.c. of this beer).

This mixture was kept at 38° C.

TABLE XXI.—*Salivary Digestion of Bread and Beer.*

	Un- changed Starch.	Soluble Starch.	Erythro dextrin.	Achroo- dextrin.	Sugar. grms.	Bread and Water.	Differ- ence.
Cold-water extract, .	all	0	0	0	0		
Totally converted, .	0	0	0	0	2·174		
Chewed, and at once examined,	much	much	fair amt.	0	0·866	·505	·139 —
Chewed, and at 38° for 30 min., . . .	„	„	much	much	·671	·706	·135 —
2 c.c. saliva at 38° for 5 min.	„	„	some	0	·314	·289	·025 +
„ 10 „	„	„	more	0	·411	·382	·029 +
„ 20 „	„	„	much	traces	·576	·476	·100 +
„ 30 „	„	„	„	„	·607	·574	·133 +
„ 45 „	„	„	„	more	·614	·639	·025 —
„ 60 „	„	„	„	„	·619	·704	·085 —
„ 90 „	less	„	„	„	·703	·726	·023 —
„ 120 „	„	„	„	much	·745	·746	·001 —
„ 150 „	„	„	„	„	·784	·769	·015 +
„ 180 „	„	„	„	„	·787	·849	·062 —

If we compare this with the digestion of starch by saliva in the presence of water, what do we find?—that an increased degree of conversion up to the end of the first 150 minutes is evident. Instead of a restraining effect on ptyalin, the beer seems to have exerted a stimulating action, and even from the earliest period the amount of sugar formed is in excess of that produced in the presence of water alone. Being more energetic

in the earlier periods, there is a falling off in the amount of sugar converted from starch after two and a half hours. Conversion begins at once, and goes a far length in the case of beer.

It might be thought that the bitterness of the beer would promote an increased salivary flow, and consequently a greater amyolysis. If it does promote a greater secretion of saliva, however, the degree of starch conversion is not hastened, as we see from the two experiments after mastication. In these the amount of sugar produced is much smaller than with water alone. The probability is that no greater secretion of saliva does take place.

XXII. *Salivary Digestion of Bread and Dilute Whisky.*

Whisky and water form one of the commonest of beverages in Great Britain, and its consumption is steadily increasing over the globe.

What effect has it on salivary digestion?

In the first set of experiments, ordinary good Scotch whisky (Talisker) was used, diluted with water in the proportion of 1 part whisky to 2 of water.

Five grm. bread crumb were mixed with 10 c.c. dilute spirit and 2 c.c. saliva (all at 38° C.) and kept at this temperature.

TABLE XXII.—*Salivary Digestion of Bread and Dilute Whisky.*

	Un- changed Starch.	Soluble Starch.	Erythro- dextrin.	Achroo- dextrin.	Sugar. grms.	Bread and Water.	Differ- ence.
Cold-water extract, .	nearly all	little	0	0	0·042		
Totally converted,	2·174		
Chewed, and at once examined, .	much	little	present	!	·328	·505	·177 -
Chewed, and at 38° for 30 min., .	much	much	much	present	·762	·706	·056 +
2 c.c. saliva at 38° 5 min.	„	vy. little	0	0	·189	·289	·100 -
„ 10 „	„	„	0	0	·291	·382	·091 -
„ 20 „	„	much	trace	trace	·473	·476	·003 -
„ 30 „	„	„	„	„	·495	·574	·079 -
„ 45 „	„	„	much	present	·619	·639	·020 -
„ 60 „	„	„	„	„	·71	·704	·006 +
„ 90 „	„	„	„	„	·724	·726	·002 -
„ 120 „	not so much	„	„	much	·737	·746	·009 -
„ 150 „	„	„	„	„	·741	·769	·028 -
„ 180 „	„	„	„	„	·75	·849	·099 -

These experiments show that weak spirit has permanently lessened the activity of ptyalin. At the end of the third hour there is still much unchanged starch present, while soluble starch and dextrins form 'much' of what remains, and sugar 0·75 gramme.

In the case of bread and water, very little unchanged starch remains at the end of the third hour, and soluble starch and dextrins are present in 'very large amounts'; while sugar forms 0·849 gramme.

Then, in the mastication of the bread, in spite of the very large (5 grammes) addition of saliva, only 0·326 gm. sugar has been formed, as compared with 0·505 gm. with water alone. After this chewed mass has been kept at 38° C. for thirty minutes, much unchanged starch is yet present and 0·762 gm. sugar, as compared with the presence of little unchanged starch and 0·706 gm. sugar in the chewed bread and water.

On the contrary, if we compare the effect of dilute whisky with that of tea, we find that the balance of favour goes to the spirit. Up till the end of the second hour, dilute whisky has a less restraining effect on ptyalin than has an infusion of tea.

XXIII.—*Salivary Digestion of Bread and Pure Whisky.*

	Un- changed Starch.	Soluble Starch.	Erythro- dextrin.	Achroo- dextrin.	Sugar. grms.	Bread and Water.	Differ- ence.
Cold-water extract, .	nearly all	little	0	0	·042		
Totally converted, .	0	0	0	0	2·174		
Chewed, and at once examined, .	chiefly	some	little	0	·45	·505	·055 —
Chewed, and at 38° C. for 30 min., .	much	much	little	present	·684	·706	·022 —
2 cc. saliva at 38° for 5 min.,	chiefly	trace	indic.	0	·166	·289	·123 —
„ 10 „	much	much	trace	0	·227	·382	·155 —
„ 20 „	„	„	„	„	·301	·476	·175 —
„ 30 „	„	„	much	?	·384	·574	·190 —
„ 45 „	„	„	„	„	·423	·639	·216 —
„ 60 „	„	„	„	present	·508	·704	·196 —
„ 90 „	„	not so much	„	much	·568	·726	·158 —
„ 120 „	„	„	„	„	·638	·746	·118 —
„ 150 „	„	„	„	„	·661	·769	·108 —
„ 180 „	„	„	not nearly so much	„	·673	·849	·176 —

XXIII. *Salivary Digestion of Bread and Pure Whisky.*

Ten c.c. undiluted whisky were mixed with 2 c.c. saliva and poured over 5 grms. bread. All were at 38° C., and kept at this temperature.

If we compare this table with the preceding, we note that pure whisky exerts a much greater action in weakening the salivary ferment than when it is diluted. In spite of 7 grammes saliva having been added during mastication, only 0.45 gramme sugar was formed, and after being kept at 38° C. for half an hour this only increased to 0.684 gramme, as compared with 0.762 gramme in the case of dilute whisky.

At the end of the first hour only 0.508 gramme sugar has been formed in the present case, as compared with 0.71 gramme in the preceding. At the end of the third hour these figures are 0.673 and 0.75 gramme. Manifestly, therefore, pure whisky has a still greater destructive action than the same when diluted.

XXIV. *Salivary Digestion of Bread and Sherry.*

The acidity of this wine was equal to 0.547 per cent., calculated as tartaric acid. The wine contained likewise 2.84 grammes sugar per cent. (=0.284 gramme per 10 c.c. wine, and this amount has been subtracted from each observation).

In this case the inhibition of amylolysis is almost complete. Starch remains entirely unconverted up to the end of the first hour, when the merest traces of soluble starch appear. Only at the expiry of two and a half hours do we find erythro-dextrin appearing, and even after three hours' digestion only 0.240 gramme sugar has been formed.

When 5 grammes bread is chewed with 10 c.c. sherry the starch undergoes no change, and the amount of sugar formed, even after such is kept at 38° C. for thirty minutes, is only 0.147 gramme.

That this inhibition of starch proteolysis is entirely due to the acid present in the wine is shown by the fact that when the sherry is neutralised and kept for one hour at 38° C. much soluble starch is present, along with tolerable amounts of erythro-dextrin and achroodextrin, while sugar forms 0.681 gramme.

On being kept at 38° C. for three hours after neutralisation, though much starch remains unaffected, there are yet large quantities of soluble starch and dextrins, and sugar forms 0·730 gramme. It is needless to state, however, that such neutralisation entirely changes the character of the wine, rendering it a nauseous turbid fluid with a semen-like odour.

XXV. Salivary Digestion of Bread and Claret—5 grammes bread, 10 c.c. good claret (Medoc), 2 c.c. saliva.

This claret possessed practically no sugar. Its acidity was equal to 0·75 per cent., calculated as tartaric acid.

The experiments showed that claret had even a greater restraining effect on salivary proteolysis than sherry. Even after three hours' digestion, the starch had undergone no conversion into soluble starch or dextrins. After ten minutes' digestion the sugar formed only amounted to 0·095 grammes; in ninety minutes 0·120 gramme, and at the end of the third hour 0·143 gramme.

The process of masticating bread with claret promotes a large flow of saliva. On examining the result, however, only a small amount of soluble starch was present, and sugar to 0·089 gramme. After keeping the same mixture at 38° C. for thirty minutes, the sugar only increased to 0·179 gramme.

Claret has therefore a most powerful effect in inhibiting salivary digestion.

On neutralising the acidity of the claret and keeping it along with bread and saliva at 38° C. for one hour, we find that much soluble starch and dextrins are present, while sugar forms 0·684 gramme. After three hours' digestion thus at 38° C. the sugar has increased to 0·73 gramme, as compared with 0·143 gramme in the case of ordinary claret.

XXVI. Salivary Digestion of Bread and Port Wine—5 grammes bread, 10 c.c. port wine, 2 c.c. saliva.

The acidity of this wine was equal to 0·427 per cent., calculated as tartaric acid. It contained 4·80 grammes sugar per cent. (0·480 gramme per 10 c.c. wine).

Of all the beverages thus examined, port wine has the greatest

effect in inhibiting starch proteolysis, with the exception of claret and sherry.

TABLE XXVI.—*Salivary Digestion of Bread and Port Wine.*

	Un- changed Starch.	Soluble Starch.	Erythro- dextrin.	Achroo- dextrin.	Sugar. grms.	Bread and Water.	Differ- ence.
Cold-water extract, .	nearly all	little	0	0	·042		
Totally converted, .	0	0	0	0	2·174		
Chewed, and at once examined, .	nearly all	0	0	0	0	·505	·505 —
Chewed, and at 38° C. for 30 min., .	much	much	fair amt.	fair amt.	·289	·706	·417 —
2 c.c. saliva at 38° 10 min.,	nearly all	some	0	0	·020	·382	·362 —
„ 20 „	„	„	0	0	·052	·476	·424 —
„ 30 „	much	much	traces	0	·116	·574	·458 —
„ 45 „	„	„	„	„	·120	·639	·519 —
„ 60 „	„	„	tolerable amount	traces	·159	·704	·545 —
„ 90 „	„	„	„	„	·223	·726	·498 —
„ 120 „	„	„	„	„	·231	·746	·515 —
„ 150 „	„	„	„	fair amt	·233	·769	·536 —
„ 180 „	„	„	„	„	·245	·849	·604 —

Inhibition is most marked throughout the whole experiments.

When chewed, the ferment in the saliva seems to be rendered almost inactive, there being no sugar produced during the process. If, after being masticated, it be kept at 38° C. for thirty minutes, 0·289 gramme sugar is formed, and this is greater than that produced by adding two c.c saliva, and allowing it to act on the bread in presence of the wine for three hours.

That this inhibition is also due to the organic acids present in the wine is manifest on neutralising it, a marked and fairly rapid conversion of starch then occurring.

In order to make a general comparison, I have drawn up the following table, which shows the results of masticating definite amounts of each of the starchy substances, and then keeping the masticated mass at 38° C. for half an hour. The sugar which has been formed from the starch by salivary proteolysis has been calculated as a percentage of the total sugar which was obtained by actual artificial conversion of the starch by acid and boiling.

TABLE XXVII.—*Comparison between Different Starchy Foods masticated, then kept at 38° C. for thirty minutes.*

Food.	Un- changed Starch.	Soluble Starch.	Erythro- dextrin.	Achroo- dextrin.	Per- centage Sugar formed.
1. White bread alone, . . .	much	much	much	much	39·28
2. Bread + water, . . .	little	„	„	„	32·47
3. Newly-baked bread + water,	much	„	„	present	34·13
4. Bread crust + water, . . .	„	„	fair amt.	„	33·0
5. Vienna bread (stale) + water,	„	„	much	much	35·14
6. „ (new) + water,	„	„	„	„	38·96
7. Bread + butter, . . .	„	„	„	„	31·27
8. „ + cheese, . . .	„	„	„	„	37·16
9. „ + milk, . . .	„	„	„	some	28·56
10. „ + broth, . . .	„	„	„	„	33·57
11. „ + tea, . . .	„	„	„	„	22·99
12. „ + coffee, . . .	„	„	„	—	29·30
13. „ + cocoa, . . .	„	„	present	present	39·83
14. „ + beer, . . .	„	„	much	much	30·86
15. „ + dilute spirits, . . .	„	„	„	present	35·05
16. „ + strong spirits, . . .	„	„	„	„	31·46
17. „ + sherry, . . .	nearly all	—	—	—	6·76
18. „ + claret, . . .	„	sm. amt.	—	—	8·23
19. „ + port wine, . . .	much	much	fair amt.	fair amt.	13·29
20. Potato, boiled and powdered,	little	—	—	much	20·28
21. „ in fragments, . . .	—	—	—	—	21·28
22. Porridge, alone, . . .	nearly all	much	much	trace	25·72
23. „ + water, . . .	some	„	sm. amt.	—	29·9
24. „ + milk, . . .	much	„	fair amt.	—	23·88
25. Rice, boiled, . . .	„	„	„	little	12·86
26. Corn flour, boiled, . . .	trace	„	much	„	38·13

CONCLUSIONS.

In order to bring this to a conclusion, attention may be drawn to the following points (which are gathered from the individual tables, and not from the concluding one):—

1. Porridge along with milk forms a more digestible compound, as far as amylolysis by saliva is concerned, than other combinations of oatmeal.

2. The more dense, the less broken down, or the firmer the jelly in which the starchy food is when undergoing salivary digestion, the less rapid and extensive is the proteolysis.

3. Some forms of starchy food undergo a certain amount of digestion by saliva, but at a certain stage this process stops, and

no matter how long they may be exposed to the action of ptyalin, no further amyolysis by saliva takes place (we must remember, however, the restraining effects which the products of digestion exert).

4. Amylaceous substances are more easily acted on by saliva when thoroughly moist than when more or less dry.

5. Bread in a light and spongy condition is more rapidly acted upon by saliva than when less spongy. Such bread, however, does not ultimately undergo any more complete digestion than does ordinary bread.

6. Milk has a retarding influence on the salivary digestion of starch in bread, while broth has little or no effect.

7. Tea has a markedly inhibitory influence on amyolysis by saliva. Coffee has this property also to a less extent. Cocoa has hardly any restraining effect.

8. Beer promotes the salivary digestion of starch.

9. Alcohol, even in dilute solution, retards salivary digestion of starch, but the action is much less marked than in the case of infusions of tea.

10. Wines have a very marked inhibitory influence on the digestion of starch by saliva, and this is almost wholly due to their acidity.

A CASE OF CROSSED DYSTOPIA OF THE KIDNEY,
WITH FUSION. By J. PLAYFAIR M'MURRICH, M.A.,
Ph.D., *Professor of Anatomy in the University of Michigan.*

ONE of the subjects used in the anatomical laboratory of the University of Michigan during the past winter presented an anomaly of the kidneys, which, on account of its infrequency, seems worthy of being reported. The case was one of crossed dystopia of the right kidney, with fusion. A description of the anomaly is as follows:—

Subject a male, 46 years old. Cause of death stated to be carbuncle. The subject was sent to the University from the Michigan Asylum for the Insane at Kalamazoo, Mich.; and the Superintendent of the asylum, Dr W. M. Edwards, has kindly supplied me with information concerning the case while under his care. The man had been an inmate of the asylum for a little over nineteen years, and was evidently a degenerate. He was subject to periods of elation, or was moody and depressed, and was filthy in his habits, and of a vicious and revengeful disposition. He suffered at times from conjunctivitis and from bronchitis, the latter during the last years of his life being at times very pronounced. The asylum records, however, show no indication of any renal troubles at any time.

Kidneys.—On opening the abdominal cavity, no trace of a kidney could be found upon the right side, but on the left side an organ larger than usual was found, from which two ureters arose. This kidney lay in the left lumbar region, its upper edge being at the usual level of the left kidney, the lower border overlapping slightly the left common iliac artery. Above, it was somewhat nearer the median line of the body than usual, overlapping about half of the abdominal aorta, but its lower portion was somewhat further laterad, the organ lying somewhat obliquely from above downwards and outwards. The drawing (fig. 1) was made after the removal of the kidney from the body, and does not represent the original relations, there having been a slight slipping downwards and inwards of the organ with reference to the aorta.

The entire organ, which showed no indications of disease, measures 14·4 cm. in length, with a diameter at its broadest part of 7·4 cm., and a thickness of about 4 cm. Viewed from the anterior surface it is seen to be distinctly composed of two portions, a lower (fig. 1, R. K.), measuring about 10 cm. in length and 6·7 cm. in breadth, and an upper (L. K.), which is comma-shaped, lying upon and embracing the upper and outer portion of the discoidal mass. This upper portion represents the left kidney, while the lower mass is

evidently the right kidney, which has crossed over to the left side of the body, and fused with the anterior surface of the lower and inner part of the left organ.

So much of the left kidney as can be seen from the anterior surface possesses the normal shape, except that its hilum is somewhat displaced, lying on the anterior surface instead of on its inner margin, and forming an elongated depression 6 cm. in length, and

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FIG. 1.—View of the kidney and vessels after removal from the body. A. 1-2, renal arteries; A_o., aorta; I. Mes., inferior mesenteric artery; L. C. I., left common iliac artery; L. C. I. V., left common iliac vein; L. K., left kidney; L. Sp. V., left spermatic vein (turned upwards); L. Ur., left ureter; R. C. I., right common iliac artery; R. C. I. V., right common iliac vein; R. K., right kidney; R. Ur., right ureter; S. Mes., superior mesenteric artery; VI.-VII., renal veins; V. C. I., inferior vena cava.

broader and deeper above than below. Its long axis is directed from above downwards and slightly outwards, its lower two-thirds lying along the outer border of the right kidney. A single ureter (L. Ur.) arises from the hilum; it possesses no well-marked pelvic dilatation, the portion of it which occupies the hilum being but little larger than the ureter proper. From the hilum it passes downwards and slightly outwards at first, lying along the outer border of the right kidney, and then directly downwards to the brim of the pelvis,

opening finally into the bladder in the normal position for the left ureter.

The right kidney, as already stated, has a discoidal shape, being somewhat longer than broad. Upon its anterior surface, rather nearer the lower than the upper border, is a hilum, which may be described as being irregularly triangular in outline, with its apex directed upwards. From the apex a well-marked groove, containing the principal vein of the organ, extends upwards and inwards to the edge of the kidney; and from the lower inner angle a similar groove, lodging the ureter and a second vein, passes downwards and inwards. The single ureter arises by four branches: one of them is directed upwards, a second upwards and outwards, and a third directly inwards. These three branches unite together to form a single trunk, with which the fourth branch, directed outwards and slightly upwards, unites to form an imperfectly developed pelvis. From this the ureter passes downwards and inwards at first, and then gradually turns directly downwards, to open finally into the bladder in the normal position of the right ureter.

The posterior surface of the entire renal mass is smooth, and shows no line of demarcation between the left and right kidneys. A shallow and broad furrow traverses it from above downwards and outwards, corresponding to what may be regarded as that portion of the left kidney which is overlapped by the right, but it does not serve to delimit the two kidneys.

Arteries.—The blood supply is furnished by seven arteries, the majority of which are of nearly the same size. (1) (figs. 1, 2, A 1) The uppermost of these is a trunk measuring about 3 mm. in diameter at its origin, which arises from the left side of the abdominal aorta, a little above the inferior mesenteric arteries, these being separated from the superior mesenteric by an interval of only 2 cm. From its origin the artery, which may be considered the left renal, passes outwards and downwards towards the upper extremity of the hilum of the left kidney, before reaching which it divides into three branches, which are distributed to the upper portion of the hilum. (2) The second artery (A 2) arises from the right side of the aorta, 2 cm. above its bifurcation into the common iliacs. It is directed at first upwards and outwards, until it reaches a point opposite the middle line of the vena cava inferior, when it curves forwards, downwards, and inwards again, and divides into two branches. One of these, the larger, passes upwards to the extremity of the groove extending upwards from the apex of the hilum of the right kidney, and there it enters almost at once into the substance of the kidney, without being prolonged to reach the hilum. The other smaller branch is directed downwards and outwards to about the middle point of the inner edge of the right kidney, where it enters a slight groove, and passes at once into the substance of the kidney. (3) A 3 arises from the left side of the aorta, about 1 cm. below the level of No. 2. It has an S-shaped course, extending first outward, and then bending inwards again to enter the posterior surface of the renal mass a little below the middle point of its vertical axis. (4) A 4 arises from the right side of the right

common iliac artery, and passing to the left and slightly downwards in front of the right common iliac, enters the kidney substance at the lower end of the groove which extends downwards and inwards from the lower inner angle of the pelvis of the right kidney. (5) A 5, which is considerably smaller than the others, arises from the inner surface of the left common iliac artery, immediately below its origin. It passes downwards and outwards, lying close to the inner side of the iliac for about 2.5 cm., and then bends somewhat abruptly outwards and enters the posterior surface of the kidney about 3.5 cm. from its

S.I

A.6

I

II

S.M

FIG. 2.—Scheme of the vascular supply. A. 1-6, renal arteries; I. Mes., inferior mesenteric artery; L.C.I. and L.C.I.V., left common iliac artery and vein; R.C.I. and R.C.I.V., right common iliac artery and vein; S. Mes., superior mesenteric artery; S.M., medial sacral artery; V.I.-V.VI., renal veins.

lower edge, first dividing into two branches, which enter close together. (6) A 6 also arises from the inner surface of the left common iliac, 3.5 cm. from the bifurcation of the aorta. Its course is similar to that of No. 5; and after dividing into two branches, it enters the posterior surface of the kidney a little below and external to that artery.

In addition to these six vessels, I noticed on the posterior surface of the organ, near its outer border, and at about the junction of its lower and middle thirds, the end of a small artery which had been

accidentally cut in removing the kidney from the body. It was not possible to be certain as to the origin of this artery, but it was probably the peripheral end of a small vessel which arose from the outer surface of the left common iliac, about 2 cm. from the bifurcation of the aorta. The peripheral end, which may be designated as No. 7, entered the substance of the kidney at the lower and inner end of a slight groove occurring at the place indicated, this groove being directed upwards and outwards, having a length of 1.3 cm., and giving passage at its outer end to a small vein.

Veins.—Altogether eight veins for the return of the blood from the kidneys were found. (No. 1) V. i. may be regarded as the left renal vein. It leaves the kidney at the upper end of the left hilum as four branches, which first unite together in pairs, and finally the two common trunks unite to form the vein, which receives just internal to its origin the left spermatic vein (fig. 1, *L. Sp. V.*). It passes under the superior mesenteric artery, and opens into the left side of the vena cava. (2) V. ii. issues from the apex of the triangular right hilum as two branches, which quickly unite to a common trunk. This, after a short course, underwent a considerable enlargement of a fusiform shape, which was occupied by a blood clot, and the vein finally opened into the left side of the vena cava, 2 cm. below the opening of No. 1. In fig. 2 the point of entrance of this vein into the vena cava is much too low down. Its true position is more accurately represented in fig. 1. (3) V. iii. was a comparatively small vein, which accompanied the upper branch of artery No. 2. It issued from the substance of the kidney at the upper extremity of the groove leading from the apex of the right hilum, and passed to the right, to open into the left side of the vena cava 2.7 cm. below the opening of vein No. 2. (4) This vein (fig. 1, V. iv.), which corresponds to the lower branch of artery No. 2, has a very different course from that just described. It issues from the outer end of the groove which receives the arterial branch, and passing almost horizontally outwards towards the left pelvis, appears to communicate with one of the branches of vein No. 2. (5) V. v. issues from the lower inner angle of the left hilum, and passes at first downwards, parallel with the upper part of the left ureter. On reaching the lower border of the kidney it curves inwards and backwards, and opens at the left side of the vena cava 4.5 cm. below the opening of vein No. 3. This vein corresponds to artery No. 4. (6) V. vi. arises by two branches which issue from the lower part of the posterior surface of the kidney, one corresponding to artery No. 5 and the other to artery No. 6. These two branches soon unite to form a common trunk, which, passing downwards and slightly inwards, opens into the outer surface of the left common iliac vein.

In addition to these, there were two other small veins which issued from the posterior surface of the kidney, but which were unfortunately cut in removing the organ from the body. One of them (No. 7) corresponded to artery No. 4, and issued from the posterior surface of the kidney about 1.3 cm. above the entrance of the artery. I was unable to trace even the probable course of this vein. The other

vein (No. 8) is the small one already mentioned as corresponding to artery No. 7, and its course was also undeterminable.

Suprarenal bodies.—Both suprarenal bodies occupied their normal positions.

A list of references to cases similar to that just described has been given by Ballowitz¹ in connection with his review of cases of complete absence of one kidney, and in the literature cited there are reports of twenty-six cases. Ballowitz discusses these cases briefly, but it has seemed to me that it would perhaps be convenient to have a more detailed tabulation of such cases for future use.

In the Table on pp. 658–9, one of the older cases mentioned by Ballowitz has not been included, as I have not been able to consult it. It is Hunter, *Med. Transact.*, iii.

Furthermore, I have omitted certain cases whose true significance is doubtful; such, for example, as that described by Portal and others, in which, although there was fusion, there was not crossed dystopia, the fused organ lying in front of the vertebral column in the mid-line of the body, as in the cases of de Neufville,² Picard,³ Pichancourt,⁴ Macdonald,⁵ and others cited by Strube.⁶

In any case of a single kidney it must be a question as to whether one has to deal with fusion of the two organs, or with an absence of one of them. I have accepted as the criterion for distinguishing between these two conditions the definition of fused kidney given by Bachhammer,⁷ and confirmed by Ballowitz. This definition may be given in Bachhammer's own words: "Eine Niere als aus zwei entstanden angesehen werden kann, wenn diese zwei Ureteren entsendet, *welche normal in die Blase münden*, während die entgegengesetzte Niere fehlt." The words which I have italicised guard against confusion with a true single kidney with a double ureter; and holding fast to this definition

¹ E. Ballowitz, "Ueber angeborenen, einseitigen, vollkommenen Nierenmangel," *Virchow's Archiv*, cxli., 1895, p. 309.

² De Neufville, *Archiv für phys. Heilk.*, 1851, p. 276.

³ Picard, *Bull. Soc. Anat. de Paris*, xlvii., 1874, p. 388.

⁴ Pichancourt, *Gazette Hebdomadaire*, 1879.

⁵ Macdonald, *Lancet*, 1885, i. 979.

⁶ See Table, No. 22.

⁷ *Ib.*, No. 15.

No.	Author.	Reference.	Sex.	Age.	Position of Fused Kidney.	Openings of Ureters into the Bladder.	Suprarenals.	Remarks.
1	PANABOLUS, .	Ci	Male.	Normal.		
2	LAVBIUS, .	Ci	Male.	Normal		
3	SANDIFORT, .	Cited by Kayer, <i>Traité des Maladies du Rein</i> , T. iii., Paris, 1841, p. 771.	Male.	...	Right.			
4	RUEZ, .	<i>Bull. Soc. Anat. de Paris</i> , viii., 1833, p. 59.	Left.			
5	BARTH, .	<i>Bull. Soc. Anat. de Paris</i> , xxviii., 1853, p. 338.	Left.			
6	GODARD, .	<i>Comptes Rendus Soc. Biol.</i> , 1856 (cited by Stoequart. See No. 14).	Male.	New-born.	Left.	Also presented atresia of rectum.
7	HILLIER, .	<i>Trans. Path. Soc. London</i> , xv., 1864, p. 43.	Male.	7 years.	Right.	...	Normal.	Mentions only one hilum.
8	JONES, .	<i>Dublin Quart. Jour. Med. Sci.</i> , xlii., 1866, p. 541.	Male.	Middle-age.	Right.	Probably normal.	...	Kidney crescentic, the lower end lying in front of the vertebral column.
9	KELLY, .	<i>Trans. Path. Soc. London</i> , xix., 1868, p. 274.	Female.	...	Right.	Normal.	...	Kidney very large.
10	DUCKWORTH, .	<i>Trans. Path. Soc. London</i> , xx., 1869, p. 283.	Right.	Normal.	...	Weight, 93 oz. Description of specimen in Pennsylvania Hospital Pathological Museum.
11	STOICESCO, .	<i>Bull. Soc. Anat. de Paris</i> , xlvii., 1874, p. 567.	Male.	9½ years.	Left.	Normal.	!	Kidney was intrapelvic in position. Statement as to suprarenals ambiguous.
12	COUPLAND, .	<i>Trans. Path. Soc. London</i> , xxviii., 1877, p. 159.	Male.	..	Left.	Normal.	Normal.	
13	GREENFIELD, .	<i>Trans. Path. Soc. London</i> , xxviii., 1877, p. 161.	Female.	19 years.	Left.	Normal.	Normal.	

14	STOCQUART, .	<i>Virchow's Archiv</i> , lxxviii., 1879, p. 244.	Male.	35 years.	Right.	Normal.	?	
15	BACHHAMMER,	<i>Arch. f. Anat. u. Phys.</i> , Anat. Abth., 1879, p. 140.	Female.	79 years.	Right.	Normal.	Normal.	
16	"	" "	Male.	...	Right.	Normal.	Normal.	Ureter from upper part of the kidney opened on left side of the bladder.
17	"	"	Male.	New-born.	Left.	Normal.	Normal.	
18	BROESIKE, .	<i>Virchow's Archiv</i> , xcvi., 1884, p. 338.	Male.	...	Left.	Normal.	?	
19	WEHN, .	<i>Virchow's Archiv</i> , xcvi., 1884, p. 354.	Male.	34 years.	Right.	Normal.	Left wanting.	Associated with complete <i>situs viscerum inversus</i> .
20	GRUBER, .	<i>Virchow's Archiv</i> , cvii., 1887, p. 489.	Male.	Middle- age.	Right.	Normal.	Normal.	Kidney somewhat cres- centic, lower end lying in front of the vertebral column.
21	KRUSE, .	<i>Deutsche. Med. Wochen- schr.</i> , xvi., 1890, p. 1158.	Male.	46 years.	Left.	Normal.	Normal.	
22	"	" "	Right.	Normal.	...	Lower half of the kidney transformed into a large hydronephrotic sack. The ureter of this por- tion of the kidney opened into the right side of the bladder.
23	BIRMINGHAM, .	<i>Dublin Journ. Med. Sci.</i> , xc., 1890, p. 47.	Left.	Normal.	Normal.	
24	PALMA, .	<i>Prager Med. Wochenschr.</i> , xvi., 1891, p. 367.	Female.	Still- born.	Left.	Normal.	Normal.	Several other abnormali- ties existed, e.g., spina bifida, scoliosis, cloaca.
25	STRUBE, .	<i>Virchow's Archiv</i> , cxxxvii., 1894, p. 227.	Male.	79 years.	Left.	Normal.	Normal.	
26	DICKINSON, .	<i>Trans. Path. Soc. London</i> , xli., 1895, p. 80.	Female.	47 years.	Left.	Normal.	...	Ureter from upper part of kidney went to right side of the bladder.
27	SCHWALBE, .	<i>Virchow's Archiv</i> , cxlvi., 1896, p. 414.	Male.	52 years.	Left.	Normal.	Normal.	Kidney crescentic, its lower part lying in front of the vertebral column.
28	The present case.		Male.	46 years.	Left.	Normal.	Normal.	

it has been necessary to exclude such cases as these described by Morgagni¹ and Blaise,² in which two ureters arose from a single kidney, both opening, however, either individually (Morgagni) or after fusion (Blaise), into the same side of the bladder. Of course, there is a possibility that such cases are really cases of fused kidney, in which the ureters are abnormal in their relations to the bladder; but where no mention is made of any peculiarity in the structure or shape of the bladder, it is preferable to consider them as cases of single kidney with doubled ureter.

Since no mention is made of the relations of the ureters to the bladder in Cases 3-7 of the table, their identification as cases of crossed dystopia with fusion must, of course, be regarded as uncertain. This is specially so with Hillier's case (No. 7), since in his description mention is made of only a single hilum. However, retaining these cases, the examination of the table reveals the following facts concerning the anomaly under consideration.

1. Out of 23 cases in which the sex is mentioned, 17, or about 78 per cent., were males, and 5, or about 22 per cent., were females. It is doubtful, however, if this represents the true proportion in the two sexes, since allowance must be made for the greater number of male subjects brought to anatomical laboratories or submitted to autopsies.

2. Crossed dystopia with fusion does not predispose to disease of the kidneys. In only one case, the second reported by Kruse (No. 22 of the table), is mention made of disease of the organ. This agrees with the statement of Strube as to the usual absence of renal symptoms in cases of dystopia, with or without fusion.

3. Out of 25 cases, the fused organ was in 10, or 40 per cent., on the right side of the body, and in 15, or 60 per cent., on the left side; in other words, in 60 per cent. of the cases the right kidney had been displaced. It is interesting to compare this with the result obtained by Ballowitz from 205 cases of absence of one kidney. In 57 per cent. of the cases it was the *left* kidney which was lacking. I have not included in the cases here considered that recorded by Wehn,³ in which the fused kidney

¹ Morgagni, "De sedibus et causis morborum." *Ep.* xxxi. 25. Eng. trans. by Alexander, vol. ii., London, 1769.

² Blaise, *Gaz. hebd. Sci. Méd.*, Montpellier, iv., 1882, p. 258.

³ Wehn, No. 19 of the Table.

was on the right side: since there was complete situs viscerum inversus in this case, it should, if counted, be regarded as a case of displacement of the right kidney, and not of the left.

4. In every case but one, in which the position of the suprarenals was accurately determined, it was found to be normal, as might be expected, since our present information on the subject of the development of the suprarenals indicates that their relation to the kidneys is merely a topographical one. The exceptional case was that recorded by Wehn.

As regards the frequency of the anomaly here considered, the relatively small number of recorded cases indicates that it is of rare occurrence. Birmingham states that Morris has noted its occurrence only once in 14,318 autopsies performed at several London hospitals.

It is practically certain that the anomaly is in all cases congenital; and it is probably in the majority due primarily to a fusion of the two metanephric blastemata, the dystopia being a result of this. It is interesting, in this connection, to note that no matter how perfect the fusion may be, each ureter seems to possess its own *clientèle* of pyramids, independent of the other, as is especially shown by the second case reported by Kruse,¹ in which, notwithstanding the hydronephrosis of the lower kidney, the parenchyma of the upper was normal. This affords support to that view of the development of the metanephros which regards the tubules as arising entirely as outgrowths of the ureter, the blastema giving rise only to the connective tissue and blood-vessels (Haycraft, *Internat. Monatschr. für Anat. u. Phys.*, xii., 1895, p. 281).

The position of the hila in the fused organs is of some interest. In the majority of cases they both occur on the anterior surface; occasionally, however, one hilum is normal in position, while the other, usually that of the crossed kidney, is on the anterior surface, and in the case recorded by Broesike² both are normal. It seemed as if a plausible explanation of the abnormal position of the hila might be found in a rotation of the kidney during its normal development, this rotation being prevented by the fusion. To test the correctness of this theory, I examined the kidney in

¹ *L.c.*, No. 22 of the Table.

² Broesike, *l.c.*, No. 18 of the Table.

a number of rat embryos (*Sigmodon hispidus*) which I possessed. Unfortunately my series was not as perfect as could be wished, but the results were as follows:—

In the youngest embryo the ureter entered the lower surface of the blastemic mass about at its middle point, if anything a little in front of this point, and extended to its centre, the blastema forming a rounded cap over the extremity of the ureter. In later stages, when the ureter had commenced to branch and to send off the primitive renal vesicles (Haycraft), a different arrangement was found. The vesicles opened into the extremity of a duct whose course was transverse to the long axis of the kidney and parallel to the horizontal plane of the body, so that

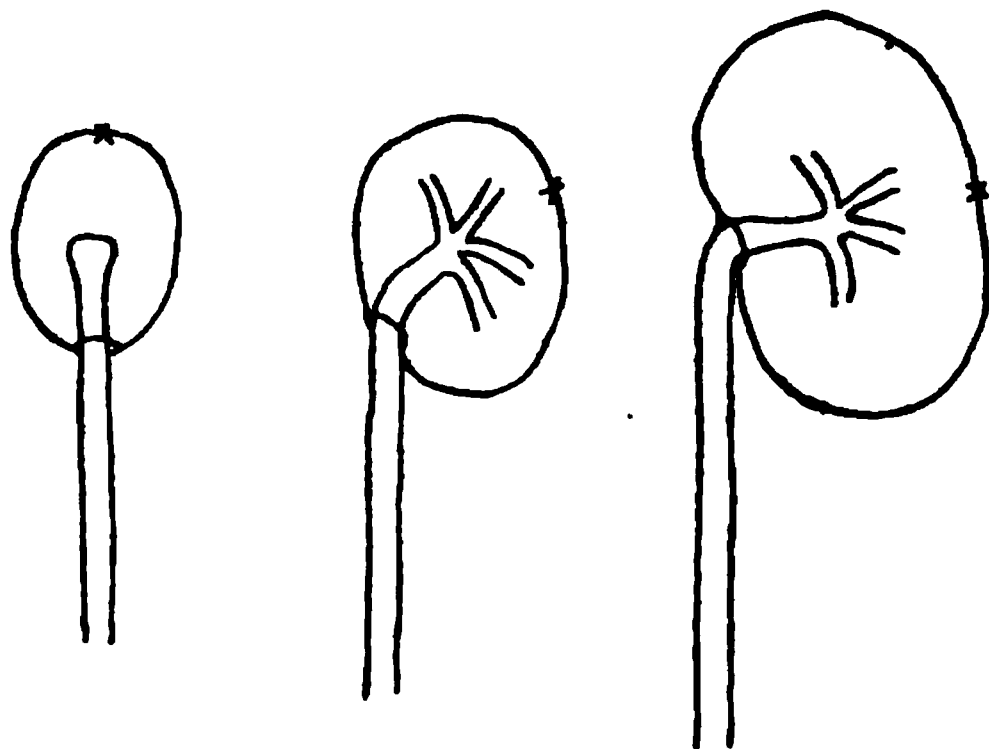


FIG. 3.—Diagrams of three stages in the development of the metanephros, showing its rotation. x Represents a presumably homologous point in each stage.

in transverse section it was cut longitudinally. This duct passed from near the centre of the renal mass towards its inner border, on reaching which it turned almost at right angles, and continued almost directly downwards as the ureter. In the oldest embryos at my disposal this condition was still existent, and I could not determine the portion of the ureter to which the transverse duct gave rise, but it may be presumed that it becomes eventually the pelvis, by a retraction, as it were, of the kidney parenchyma from around it. The conditions may be understood from an inspection of fig. 3, in which they are represented diagrammatically, and from which it may be seen that a rotation of the kidney substance does

apparently occur, the original apex of the blastemic mass rotating outwards until it occupies approximately the middle of the convex border of the kidney. In case of fusion at an early stage this rotation would be prevented in both kidneys, since each normally would rotate in an opposite direction, and the subsequent retraction of the kidney parenchyma from the transverse duct would bring it to the surface as the pelvis, on the anterior surface of the kidney. When, however, the fusion occurred at a later stage of development, when the rotation had progressed to some extent, it might be continued in one kidney, thus bringing about a reversal of the rotation in the other, usually the crossed kidney, and the final location of the hilum on its anterior surface. And finally, should the fusion be postponed until the rotation was complete, such a condition as that seen in Broesike's case would be produced.

The position of the hila in the case recorded by Wehn is of exceptional interest. The two hila were situated on the *posterior* surface of the organ! I may quote Wehn's own words, which are to the effect that the right kidney "hat die Gestalt einer biconvexen Scheibe, die Gestalt der Milz; und ebenso wie bei dieser der Hilus nicht am Rande, sondern in der Mitte des einen Fläche hervortritt, so ist auch in dieser Niere der Hilus in der Fläche und zwar der hinteren, dem Musculus quadr. lumb. zugekehrten, Fläche gelegen." I have found in the literature no similar case, and it must be supposed that it has its origin in the causes which have produced the situs inversus with which it is associated. The fact that the hila are 180° distant from where they are usually found in fused kidneys, seems highly suggestive in connexion with the question as to the proximate cause of situs inversus viscerum.

The occurrence of crescentic kidneys, whose lower ends lie in front of the vertebral column, would indicate that the anomaly here considered belongs primarily to the same category as do horseshoe kidneys; causes, of which we know nothing, determining the crossed dystopia. Broesike's case, however, to judge from the position of the hila, indicates that, in some cases at least, the lower end of one kidney may be fused with the upper end of the other, and this may be true in the majority of cases. It is noteworthy that in fourteen out of seventeen cases, *i.e.*, in

about 82 p.c. of the cases in which the relation could be determined, the ureter of the uppermost kidney opens into the right side of the bladder when the fused organ is on the right side, and into the left side when it is on the left; the three cases in which the reverse occurred being the second cases of Bachhammer¹ and Kruse,² and the cases of Dickinson³ and Wehn.⁴

Finally, mention may be made of the abnormality of the blood supply in these abnormal kidneys. In comparatively few of the cases reported has a thorough description of the veins and arteries been given, but when this has been done, they are usually abnormal both in number and position, it being especially noteworthy that branches frequently pass to the kidneys from one or both of the common iliac arteries.

¹ Bachhammer, *l.c.* No. 16 of the Table.

² Kruse, *l.c.* No. 22 of the Table.

³ Dickinson, *l.c.* No. 26 of the Table.

⁴ Wehn, *l.c.* No. 19 of the Table.

THE DUODENO-JEJUNAL FLEXURE: ITS VARIATIONS AND THEIR SIGNIFICANCE. By N. BISHOP HARMAN, B.A., M.B., M.R.C.S., *St John's College, Cambridge; Demonstrator of Anatomy, Cambridge University.*

I HAVE been led to make some investigations into the anatomy of this region, owing to the finding of the unusual form of the flexure described below and delineated in figure 1.

(1) *Present Descriptions.*

The descriptions of the flexure and the commencement of the jejunum vary considerably in the special monographs on the intestinal canal, and in articles on the part in the text-books. All give fairly full descriptions of the suspensory ligament, or muscle of Treitz, to which the flexure is due.

Treves (1), in his Hunterian lecture of 1885, gives several figures of the flexure, but does not refer to any usual course taken by the commencing jejunum; the figures mostly show a leftward tendency; whilst one, that of a spider-monkey (fig. 1, B), seems to indicate a rightward position of the part.

Jonnesco (2) makes no special reference to the direction of the part, but figures it in that position which appears to be the most common, viz., curving to the left of the median line. In his section of *Poirier's Anatomy*, he states that "the jejunum commences at the level of the duodeno-jejunal flexure, passing forwards and downwards to the left; thence it makes a curve from left to right."

In other text-books I find the following variations in description. Macalister (3) states that "at the flexure the gut makes a sharp bend forwards and leftwards."

Sappey (4): that "the gut passes forwards and to the left, making, with its continuation downwards and to the right, a semi-circular curve." This agrees substantially with Jonnesco, and also with Gegenbaur (5).

Cunningham (6): that "the jejunum bends suddenly forwards and downwards upon the duodenum, forming the flexure."

Holden (7): that "the jejunum begins by an abrupt downward bend."

Quain, Morris, Gray, Cleland and Rauber make no special mention of the part.

These extracts show that the usual description may be ranged under three forms:—

1. That which bends forwards and to the left in a fairly wide curve, thence passing downwards and to the right.
2. That which bends forwards, downwards, and to the left in a sharp curve.
3. That which bends directly forwards and downwards along the line of the fourth part of the duodenum.

In the series of subjects which I have examined, I have found all these forms represented, and in addition two other forms in which a slight and a well-marked bend to the right side of the body was exhibited. The position found was in each case a fixed one, and not subject to the movements of the intestines.

(2) *Description of Special Cases.*

Figure 1 represents the condition of the flexure found in a dissecting-room subject (male, aged 72 years).

It shows a rightward bend of the commencing jejunum of a pronounced character. The examination was made immediately at the time of the opening of the great sac, before any dissection had been attempted. The abdominal viscera had an especially healthy appearance, and there was a complete absence of inflammatory adhesions, so that this common source of displaced relations could not apply here.

From the pylorus to the free part of the jejunum, the gut followed a very tortuous course, altering its direction no less than eleven times.

From the pylorus to the usual site of the flexure there were four prominent knuckles formed by these bends. The gut passed first laterally beneath the edge of the liver, thence dorsally and mesially to become retro-peritoneal: the lesser curvature of the

FIG. 1.—Subject, male, aged 72 years. *, retro-peritoneal commencement of jejunum, passing column transversely from left to right, at level of 2nd lumbar vertebra. *Dd.*, duodenum. *Jj.*, jejunum, with free mesentery. *S.M.vs.*, superior mesenteric vessels. *Pp.*, parietal peritoneum. *Tr.Mc.*, site of transverse meso-colon. *H.F.*, site of hepatic flexure. *D.C.*, site of ascending colon. *Lc.*, liver. \times , site of orifice of bile papilla. *St.*, stomach. *Cn.*, annular constriction of stomach. *Py.*, pylorus. *C.M.*, costal margin. *R.X.*, site of 10th costal cartilage. α , fossa duodeno-jejunalis. β , fossa para-duodenalis. γ , dotted line indicates site of freedom of gut from dorsal parietal peritoneum. δ , site of the colic loop.

stomach could be found to be continuous with the mesial edge of the gut, as found for other cases by Mr Young of Liverpool (8). Further, the gut passed obliquely and downwards across the ventral surface of the kidney, reaching to within half an inch of its lateral border; it was here dorsal to a short length of ascending meso-colon, which held a considerable loop of the ascending colon lying in the belly cavity, with its convexity directed towards the middle line. Thence the gut retraced its course, making a sharp upward turn to reach the level of the pylorus, as high as the first lumbar vertebra. From this point it followed the usual course of the duodenum, presenting descending, transverse, and 'fourth' divisions, and reaching upwards on the left side of the column to the second lumbar vertebra; at this point it was inferior to the line of attachment of the meso-colon. Instead of becoming free jejunum at this place the gut passed across the column transversely, lying on the second lumbar vertebra, reaching the left side of that vertebra, and was for this distance (about 2 inches) beneath the dorsal parietal peritoneum, and immediately ventral to and in contact with the pancreas and superior mesenteric vessels.

The jejunum then became gradually movable as its mesentery formed and lengthened, the direction of the first part of the parietal mesenteric attachment being obliquely from right to left. The whole length of the retro-peritoneal gut, from pylorus onwards, measured about 13 inches.

On the upper and left side of the flexure was a well-marked peritoneal pouch, having a mouth $\frac{3}{4}$ inch in breadth, and a depth of $\frac{1}{4}$ inch; its mouth was directed toward the right side; it did not penetrate beneath the retro-peritoneal part of the jejunum. It doubtless represented a 'fossa duodeno-jejunalis'; it was noticeable that the direction of its mouth was altered in a manner consistent with the displacement of the jejunal gut.

A shallow 'para-duodenal pouch' existed alongside the *arteria colica sinistra*. The subject also presented a well-marked hour-glass constriction of the stomach, which was formed by a complete annular thickening of muscle of considerable substance, dividing the stomach at the junction of the middle and right thirds of its axis into a left chamber of about four-fifths and a right of about one-fifth of its total capacity.

The case delineated in figure 2 was also from a dissecting-room subject (male, aged 46 years), and was found at an interval of three months after the former case. The gut in this case differed only from the preceding in the absence of complication in the duodenal part. It passed through its usual bends, and the shortness of its third part caused it to assume rather a 'V' shape. It agreed with the foregoing case in---

(A) The continuance of the gut beneath the dorsal parietal peritoneum, across the column at the second lumbar vertebra,

FIG. 2.—Subject, male, aged 46 years *, retro-peritoneal jejunum. *Id.*, duodenum. *Jj.*, jejunum with mesentery. *Ms.*, mesentery. *S.M.vs.*, superior mesenteric vessels. *Ao.*, aorta. *Pp.*, parietal peritoneum. *Tr.Mc.*, transverse meso-colon. *Pa.*, pancreas. *a*, fossa duodenalis superioris. *β*, a twig from art. colica sinistra which is within the edge of the above fold. Below the superior fossa is a small inferior fossa. *γ*, dotted line indicating the extent of the superior fossa. *δ*, dotted line indicating site of freedom of gut from dorsal parietal peritoneum.

for about 1½ inches, becoming then free of the wall, save for its controlling mesentery, which in its attachment followed a like oblique leftward and downward direction in its early part.

(B) The complication of the ascending colon by a considerable loop of gut, which was in this case situated at its highest part, close to the hepatic flexure, making the latter to appear as if

double. The convexity of the loop was directed downwards, forwards, and mesially.

(C) The complete absence of any pathological peritoneal adhesions.

Two fossæ were present in the neighbourhood of the flexure, which are indicated in the figure. The upper fossa, 'superior duodenal,' was remarkably large.

Since the finding of the first described case, I have examined nineteen others, noting the condition of the flexure and the condition of the ascending colon, whether straight or complicated by loops. In each case the examination has been made immediately on opening the belly.

I found variations which account for the differences in the descriptions of the several writers quoted above, besides a further case in which a rightward tendency was shown, though not to such a degree as in the two detailed cases.

(3) *Table of Varieties.*

Form.	No. of Cases.	Direction of Bend.	Condition of Ascd. Colon.
1.	Four.	Directly to left flank in a bold curve, then downwards. Bend to left = 1 to 2 inches in a descent of 1 inch.	Straight.
2	Eight.	Forwards, downwards, and to the left, then downwards. Bend to left = $\frac{1}{2}$ to $\frac{3}{4}$ inch in descent of 1 inch.	Straight.
3.	Six.	Forwards, then straight down on duodenum.	Straight.
4.	One.	Forwards, then downwards on anterior surface of column, tending to right side $\frac{1}{2}$ inch in descent of 2 inches.	Straight.
5.	Two.	Cases detailed: — Forwards, transversely to right side, and retro-peritoneal.	Complicated by loops.

From the foregoing table, it will be seen that the leftward position (Nos. 1 and 2) occurred in twelve cases, and that it is considerably more common than any other form; the direction forward and straight down (No. 3) following with six cases. The rightward position was found in three; though in these, the

two described at length must be separated from the one in the fourth class, where the tendency rightward was but slight, and the jejunum possessed a mesentery from the flexure ; it was, however, fixed in its rightward position by the meso-colon, which crossed it.

(4) *The Significance of the Variations.*

The two detailed cases are, I think, of interest beyond their importance as variations ; for the production of the conditions here found, viz., loss of a normally present mesentery and the deflected position, may be found to bear on the question as to the means whereby the duodenum normally loses its original mesentery, and becomes retro-peritoneal in man.

The processes of peritoneal distribution have been accounted for by the enunciation of two theories:—

(1) O. Hertwig's theory of adhesion of continuously approximated peritoneal surfaces (9).

(2) Treves' theory of peritoneal traction (10).

The former theory postulates a deflection of the duodenum by the over-passing cæcum ; the deflected duodenum being applied to the body wall loses its mesentery first by the adhesion, and secondly by the absorption of the contiguous peritoneal surfaces. Such a theory would account for the loss of the jejunal mesentery in the above cases, if we can first explain the rightward displacement of the gut. There is, however, no over-passing colon, such as diverts the duodenum ; there is no pressure from the left, but apparently rather the reverse, as the great gut was more extensive on the right side than is normal, so that it actually pressed upon the small gut from that side by the extra colic loops described above.

On the other hand, Treves, whilst recognising the possibility of the adhesion, and subsequent absorption of approximated surfaces of peritoneum in some parts, believes that this is not the process whereby the duodenum loses its mesentery, but rather that it is due to an insufficient supply of peritoneal covering afforded to the rapidly growing cæcum and great gut ; so that the cæcum in its descent from the region of the pylorus tends to draw away any redundant peritoneum such as will exist on the deflection of the duodenum.

In these two cases there was an excessively long ascending colon, which seems to indicate that the growth rightward and downward of the great gut was greater than usual. This would, in the terms of Treves' theory, cause the requisition of further peritoneum from the dorsal parietes. Now, the extremity of the duodenum is fixed by its suspensory band, so that it cannot be further displaced, but ample supplies could be afforded to the great gut if its lateral and downward traction force were sufficient to retract the redundant peritoneum of the jejunal mesentery immediately succeeding the duodenum. That the colon could effect such a further traction seems a reasonable conclusion, more especially as this traction would at the same time produce the rightward deflection of the 'bared' jejunum, which would otherwise remain unexplained.

In the absence of any evidence as to the existence of some directing influence, such as Hertwig's theory would require, to cause the rightward displacement of the jejunum, and on the existence, on the contrary, of the general tendency which the presence of the large liver must have in keeping the upper part of the gut to the left side, these two cases, with their rightward direction, retro-peritoneal position, and coincident elongated and looped ascending colon, must, I think, be allowed to lend considerable support to the theory of peritoneal traction, as propounded by Treves.

The supposition that the colic loops indicate an excessive growth is, I think, warranted by the coincident excess in size of the duodenum in the first case, also by reason of the chambered stomach,¹—if we may accept Wiedersheim's suggestion (13) that a bilocular stomach is a progressive feature,—but chiefly by reason of the uncomplicated condition of the colon in all the other cases.

(5) *Attempt at Experimental Production.*

I have attempted experimentally to determine whether manual traction on the upper part of the hepatic flexure would produce a displacement of the commencement of the jejunum and unfold its mesentery.

¹ On bilocular stomach, see Keith, *Jour. Anat.*, April 1898, p. 456.

The subject used was a female, aged 18 years, deceased only one day. The commencement of the jejunum occupied the 'third' position, *i.e.*, forwards and downwards. No peritoneal fossæ were present. The ascending colon was straight.

A wooden clamp, 3 inches in length, was fixed to the colon immediately below the hepatic flexure; steady traction was exerted thereon in a rightward and downward direction by means of a spring balance. The colon rapidly acquired a mesentery, and the jejunal mesentery shifted its position on the parietes so that the small gut lay transversely to the column. At this point the balance registered a tension of 10 lbs. The peritoneum now unfortunately tore, leaving the colon free. The jejunal mesentery was not unfolded by the pulling, but subsequent gentle traction with the finger-tips easily displaced it, so that the gut became retro-peritoneal,—thus, at any rate, showing how easily peritoneal displacement may be effected.

(6) *Embryological Evidence.*

I have examined the literature of the development of the part, hoping that it might throw some light on the subject, but there does not appear to be any very definite information.

His's figures (11) seem to indicate that as soon as the various parts of the alimentary canal are differentiated, that which will be the first part of the jejunum occupies a position to the left of the median line, from which it passes into the loose coils of gut by a gentle curve downwards from left to right.

Dexter (12), in a recent communication on the subject, says that after the recession of the gut from the ventral hernia, "the jejunum usually forms a simple loop towards the right side of the embryo." Apparently this description refers to the jejunum as a whole, so that one cannot make use of the observation here.

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NOTES ON A SERIES OF THIRTY-NINE CASES OF
MECKEL'S DIVERTICULUM. By LOUIS J. MITCHELL,
M.D., *late Coroner's Physician, Chicago.*

THE writer having made a number of necropsies, and having searched for this diverticulum in each one, presents the following notes as a contribution to the statistics of its frequency of occurrence.

In all, 1635 bodies were examined. Of these, 1330 were males, and the diverticulum was present thirty-five times; of the 305 females, it was present in only four.

The cases were as follows:—

CASE 1.—Male, æt. 45. Death from morphine poisoning. Tubular diverticulum, full calibre of intestine, 2 inches long, 24 inches from valve, mesentery nearly to tip.

CASE 2.—Male, æt. 19. Death from fracture of skull. Tubular diverticulum, full calibre of intestine, $1\frac{1}{2}$ inches long, 36 inches from valve.

CASE 3.—Male, æt. 23. Death from fracture of skull. Tubular diverticulum, full calibre of intestine, $2\frac{1}{2}$ inches long, 30 inches from valve.

CASE 4.—Male, æt. 50. Death from cardiac aneurism. Cord-like diverticulum, tip attached near internal abdominal ring, $2\frac{1}{4}$ inches long, patent for $\frac{1}{4}$ inch, 6 inches from valve.

CASE 5.—Female, æt. 24. Death from peritonitis. Tubular diverticulum, full calibre of intestine, 1 inch long, 15 inches from valve, arising from side of gut.

CASE 6.—Male, æt. 23. Death from stab wound. Tubular diverticulum, full calibre of intestine, $3\frac{1}{2}$ inches long, 35 inches from valve.

CASE 7.—Male, æt. 35. Death from fatty heart. Tubular diverticulum, 1 inch in diameter, $1\frac{1}{4}$ inches long, 34 inches from valve.

CASE 8.—Male, æt. 33. Death from empyema. Tubular

diverticulum, 1 inch in diameter, 1 inch long, 15 inches from valve.

CASE 9.—Male, æt. 23. Death from bullet wound. Conical diverticulum, 2 inches in diameter at base, 2 inches long, 16 inches from valve, mesentery half way to tip.

CASE 10.—Male, æt. 38. Death from bullet wound. Tubular diverticulum, $\frac{1}{4}$ inch in diameter, $\frac{1}{2}$ inch long, 36 inches from valve.

CASE 11.—Female, æt. 26. Death from fracture of the skull. Tubular diverticulum, 1 inch in diameter, 2 inches long, 24 inches from valve. Mesentery to tip, pointing towards head, lying on top of intestinal coils.

CASE 12.—Male, æt. 49. Death from morphine poisoning. Conical diverticulum, 2 inches in diameter at base, 3 inches long, 36 inches from valve.

CASE 13.—Male, æt. 4 months. Death from inanition. Conical diverticulum, $\frac{3}{4}$ inch in diameter at base, $\frac{3}{4}$ inch long, 16 inches from valve, arising from side of gut close to mesentery.

CASE 14.—Male, æt. 41. Death from alcoholism. Tubular diverticulum, 1 inch in diameter, 2 inches long, 26 inches from valve.

CASE 15.—Male, æt. 27. Death from prussic acid poisoning. Conical diverticulum, 2 inches in diameter at base, 1 inch long, 24 inches from valve; mesentery half way to tip.

CASE 16.—Male, æt. 45. Death from fracture of skull. Tubular diverticulum, $\frac{3}{4}$ inch in diameter, 1 inch long, 30 inches from valve.

CASE 17.—Male, æt. 41. Death from alcoholism. Inverted conical diverticulum, $1\frac{1}{2}$ inches in diameter at free edge, 1 inch at attachment to bowel, 3 inches long, 36 inches from valve. Intestines adhering to each other by firm adhesions; diverticulum also adherent to loop of intestine.

CASE 18.—Male, æt. 60. Death from alcoholism. Tubular diverticulum, 1 inch in diameter, 2 inches long, 20 inches from valve. Adhering to mesentery of intestine, and pointing towards head.

CASE 19.—Male, æt. 23. Death from bullet wound. Tubular diverticulum, 1 inch in diameter, 3 inches long, 36 inches from valve: Mesentery nearly to tip.

CASE 20.—Male, æt. 8. Death from bullet wound. Tubular diverticulum, $\frac{1}{2}$ inch in diameter, 1 inch long, 20 inches from valve. Small secondary diverticula from tip.

CASE 21.—Male, æt. 45. Death from bullet wound. Tubular diverticulum, 1 inch in diameter, 4 inches long, 36 inches from valve. Two large secondary diverticula at tip.

CASE 22.—Male, æt. 28. Death from bullet wound. Conical diverticulum, 3 inches in diameter at base, 3 inches long, 35 inches from valve.

CASE 23.—Male, æt. 55. Death from alcoholism. Tubular diverticulum, 1 inch in diameter, 4 inches long, 30 inches from valve. Adhering to mesentery of intestine, and pointing towards head.

CASE 24.—Male, æt. 42. Death from bullet wound. Tubular diverticulum, full calibre of intestine, 2 inches long, 18 inches from valve.

CASE 25.—Male, æt. 22. Death from enteric fever. Tubular diverticulum, full calibre of intestine, $1\frac{1}{2}$ inches long, 30 inches from valve. No ulcers in diverticulum.

CASE 26.—Female, æt. 50. Death from alcoholism. Tubular diverticulum, 1 inch in diameter, 2 inches long, 35 inches from valve.

CASE 27.—Male, æt. 35. Death from pulmonary tuberculosis. Hammer-shaped diverticulum, 2 inches in width at tip, $1\frac{1}{2}$ inches long, 36 inches from valve. Adhering to mesentery of intestine.

CASE 28.—Male, æt. 52. Death from nephritis. Tubular diverticulum, full calibre of bowel, $1\frac{1}{2}$ inches long, 30 inches from valve. Adhering to mesentery of intestine by slight adhesions, pointing towards head.

CASE 29.—Male, æt. 20. Death from pulmonary hæmorrhage. Tubular diverticulum, $1\frac{1}{4}$ inches in diameter, $2\frac{1}{2}$ inches long, 38 inches from valve.

CASE 30.—Male, æt. 57. Death from endocarditis. Tubular diverticulum, $1\frac{1}{4}$ inches in diameter, $2\frac{1}{2}$ inches long, 20 inches from valve.

CASE 31.—Male, æt. 46. Death from cerebral apoplexy. Tubular diverticulum, 1 inch in diameter, $2\frac{1}{2}$ inches long, 21 inches from valve.

CASE 32.—Male, æt. 38. Death from railroad accident. Globular diverticulum, 2 inches in diameter, 38 inches from valve.

CASE 33.—Male, æt. 55. Death from valvular disease. Tubular diverticulum, $\frac{3}{4}$ inches in diameter, 4 inches long, 40 inches from valve.

CASE 34.—Male, æt. 42. Death from diabetes. Cord-like diverticulum, $\frac{1}{8}$ inch in diameter, $1\frac{1}{2}$ inches long, 8 inches above valve; tip free.

CASE 35.—Female, æt. 60. Death from enteritis. Tubular diverticulum, $\frac{3}{4}$ inch in diameter, 1 inch long, 30 inches from valve. Arises from side of intestine.

CASE 36.—Male, æt. 16. Death from bullet wound. Tubular diverticulum, 1 inch in diameter, $1\frac{1}{2}$ inches long, 30 inches from valve.

CASE 37.—Male, æt. 53. Death from bullet wound. Conical diverticulum, 1 inch in diameter at base, 1 inch long, 31 inches from valve.

CASE 38.—Male, æt. 32. Death from morphine poisoning. Tubular diverticulum, $\frac{3}{4}$ inch in diameter, $2\frac{1}{2}$ inches long, 37 inches from valve; small secondary diverticula at tip.

CASE 39.—Male, æt. 38. Death from asphyxiation by illuminating gas. Tubular diverticulum, 1 inch in diameter, 2 inches long, 33 inches from valve.

It seems worthy of note that 7 of the cases occurred in Poles, though no unusual number of this nationality was examined; and while 109 negroes were examined, the diverticulum was found but once (No. 37).

As regards contents, 2 contained soft fæces; the others were either empty or contained flatus. All the specimens met with came off at right angles to the bowel. Oderfeld has pointed out that the presence of congenital malformations—hare-lip and the like—in patients with symptoms of intestinal obstruction renders it possible in some cases to diagnose the obstruction as being due to the presence of a diverticulum. In none of the present cases was any such malformation found.

Finally, attention may be directed to the extreme irregularity with which this diverticulum is found. The average yearly number of necropsies was 400. On two occasions they occurred on successive days, while at other times one or two hundred bodies might be examined without finding one.

**CONGENITAL ABNORMALITIES OF THE HEART IN
THE INSANE** By FRANCIS O. SIMPSON, L.R.C.P. Lond.,
F.R.C.S. Eng., *Pathologist and Assistant Medical Officer to
the West Riding Asylum, Wakefield.*

THE occurrence of four cases of redundancy of the pulmonary valves during the past two years, and the discussions consequent thereon, have led to the investigation which forms the basis of this paper. When the first of these abnormalities was noticed,

FIG. 1.—Right ventricle, opened, showing four pulmonary semilunar valves,
Case 46.

the senior members of the staff who were present expressed the opinion that it was the only case of the kind which had been seen in the post-mortem room of the West Riding Asylum, Wakefield, and upon examination of the records such proved to be the case.

It has been suggested to me from an outside source that these abnormalities of the heart are comparatively common, and that

the paucity of instances recorded is due to the fact that the cases are not written up at the time of the autopsy, and subsequently the smaller details of interest, such as patency of the foramen ovale, or non-pathological anomalies of the various valves, may be omitted. This source of fallacy may, however, be eliminated in the present series of cases; the appearances noted are always dictated by the medical officer to a clinical

Fig. 2.—Right ventricle, opened, showing four semilunar pulmonary valves,
Case 44.

clerk at the time of examination, and such has always been the custom in this institution.

In the present paper a period of thirty-one years will be considered, and a total of 4252 necropsies, of which 2496 were conducted upon male subjects and 1756 upon female. Congenital abnormalities of the heart were found present in 148 cases of the total number, or 3.48 per cent.; 103 of these cases were in males, or 4.12 per cent., and 45 in females, or 2.56 per cent.

It may be alleged that these figures, dealing as they do with an insane community, are very different from those which would be obtained by an analysis of the post-mortem records of a general hospital, and such may possibly be the case. It is only reasonable to suppose, however, that such anomalies will be more common among the insane than amongst those at large, surrounded as we are in these institutions by the various stigmata of degeneracy. Unfortunately, I have been unable to find any definite data upon which to establish a comparison, and can only hope that the pathologist of some large general hospital may at some future time give the profession the benefit of his experience.

Amongst the various forms of congenital abnormalities of the heart, fenestration of the various valves stands out pre-eminently as the most common, and appears to have no baneful influence upon the duration of life, nor to give rise to any untoward symptoms when unaccompanied, as is usually the case, by valvular insufficiency, of which the reticulation may be either the cause or an ineffective concomitant. In 101 cases the various valves of the heart were found more or less fenestrated, equivalent to 2·37 per cent.; but the most striking fact is the vast difference in the number of cases as divided between the two sexes, 84 examples, or 3·36 per cent., occurring amongst the males, whilst only 17 cases, or ·96 per cent., were females.

The following table shows at a glance the frequency of this anomaly as distributed among the various cardiac valves:—

	Total.	Male.	Female.
Fenestrated aortic,	75	63	12
„ pulmonary,	18	16	2
„ mitral,	6	5	1
„ tricuspid,	2	..	2
Totals,	101	84	17

It will be noticed how much more frequent this condition is in the aortic valves than in any other situation—four times more frequent than in the pulmonary; also that the male sex shows

the anomaly five times as often as the female. In the case of the pulmonary valves the males are affected three times as often as the females, and in the mitral valve five times as often as the females, though the latter valve is only affected once for every twelve times that its fellows on the same side of the heart are found reticulated. Lastly, the tricuspid valve will be seen to be fenestrated much the most seldom—in only two instances, both of the female sex.

Into the exact average of the ages at death and mental condition of these cases it has seemed unnecessary to enter. Suffice it to say that all clinical forms of insanity and every period of life are represented in their category so equally that an exact analysis would be a waste of time and space.

Having disposed of the cases of fenestrated valves, it will be seen how tremendously our numbers are diminished, showing the great rarity of congenital abnormalities of the heart in the insane. Out of 4252 post-mortem examinations upon the two sexes, only 47 cases of congenital structural defect remain: 19 of these occurred in the 2496 males, and 28 in the 1756 females. The average age at death for both sexes was 47 years: in the males 50·6 years, and in the females 44·4 years. [The average age of all persons dying in the asylum during the years 1894 and 1895 was 49·5 years for both sexes: 48 years for males, and 51 years for females.] The mental states at the time of death are shown in the subjoined table:—

	Totals.	Males.	Females.
Congenital defect with epilepsy,	2	1	1
" " without epilepsy,	4	1	3
Epileptic dementia,	4	2	2
General paralysis,	8	4	4
Acute mania,	2	...	2
Chronic mania,	3	2	1
Recurrent mania,	1	...	1
Acute melancholia,	3	2	1
Chronic melancholia,	6	1	5
Primary dementia,	1	...	1
Secondary dementia,	9	3	6
Senile dementia,	4	3	1
Totals,	47	19	28

In none of these 47 cases was the condition of the heart diagnosed during life from symptoms exhibited ; and in only 9 of the total—viz., 3 males and 6 females—were there any symptoms of cardiac lesion before death, these signs being invariably those of some coexisting pathological state rather than of the congenital defect.

By far the most common of these abnormalities was patency of the foramen ovale, which occurred in 27 instances, or 37·45 per cent. of the total,—the males being 9 in number, or 19·15 per cent., and the females 18, or 38·3 per cent. Thus it will be observed that this defect is just twice as common in women as in men. The ages at death for both sexes averaged 48 years; that of the males being 54·5 years, and of the females 44·2 years. The mental conditions at the time of death are shown in the subjoined table:—

	Totals.	Males.	Females.
Congenital defect with epilepsy, . . .	2	1	1
" " without epilepsy, . . .	3	...	3
Epileptic dementia,	4	2	2
General paralysis,	5	1	4
Acute mania,	1	...	1
Chronic mania,	1	1	...
Acute melancholia,	1	...	1
Chronic melancholia,	3	...	3
Secondary dementia,	4	2	2
Senile dementia,	3	2	1
Totals,	27	9	18

Out of these 27 cases, cardiac symptoms were only observed in 3 during life,—2 of these being men, and the third a woman ; and they were always those of some accompanying cardiac lesion.

Having thus eliminated the commoner varieties of cardiac anomalies, we come to the more interesting cases of valvular deficiency, or redundancy, as the case may be ; and 20 examples of these remain for our consideration out of the 4252 necropsies, 10 of either sex,—the average ages at death being 45·75 years

for both sexes; 47 years for the males, and 44·5 years for the females. The mental conditions at death are shown in the following table:—

	Totals.	Males.	Females.
Congenital defect with epilepsy,	1	1	...
General paralysis,	3	3	...
Acute mania,	1	...	1
Chronic mania,	2	1	1
Recurrent mania,	1	...	1
Acute melancholia,	2	2	...
Chronic melancholia,	3	1	2
Primary dementia,	1	...	1
Secondary dementia,	5	1	4
Senile dementia,	1	1	...
Totals,	20	10	10

In 1 male and 4 female cases only out of the above 20 were any symptoms noticed during life, viz., *Case 2*, a female, in which the pulmonary valves were adherent to one another and the orifice smaller than average, the symptoms being those of valvular incompetence; *Case 5*, a female, the valvular anomaly being a tricuspid, with one large and one small valve segment, and the symptoms those of insufficiency; *Case 16*, a male, in which there were only two cusps to the aortic valve, and the symptoms were those of aortic regurgitation; *Case 24*, a female, in which there was the same abnormality, with symptoms of aortic incompetence and obstruction; and *Case 37*, a female, in which the pulmonary valve possessed four segments, but the patient died from mitral obstruction.

Reference to the following table will show the valve which is abnormal in each case, and the nature of the anomaly, together with the sex, age, and mental state at death of the patient, and the causes of death, as certified in the medical certificate.

With regard to frequency, it will be observed that in 8 cases, 6 males and 2 females, the aortic valves are affected; the pulmonary valves are the next most common site of abnormality, their cusps being affected in 6 instances, 2 males and 4 females; after these comes the mitral, 4 cases, 1 male and 3 females; and,

Cases of Anomalies of the Valves of the Heart in the Insane.

No. of Case.	Sex.	Age at Death.	Cardiac Valvular Abnormality.	Mental State at Death.	Certified Cause of Death.
1	M.	31	Aortic cusps adherent to one another, only attached to A. by bases.	Acute melancholia.	Phthisis pulmonalis.
2	F.	28	Pulmonary cusps adherent to one another and orifices contracted,	Secondary dementia.	Morbus cordis.
3	F.	26	Two cusps of pulmonary united and division rudimentary,	Primary dementia.	Phthisis pulmonalis.
4	M.	60	One flap of mitral small and rudimentary,	Chronic mania.	Chronic brain atrophy.
5	F.	57	One large and one small flap to tricuspid,	Secondary dementia.	Chronic brain atrophy and morbus cordis.
6	M.	40	Two cusps to aortic valve, posterior larger,	Acute melancholia.	Pneumonia.
16	M.	67	Two cusps to aortic valve,	Idiocy.	Chronic brain atrophy and morbus cordis.
17	M.	37	Two cusps to aortic valve,	Dementia of general paralysis.	General paralysis.
18	F.	44	One flap of mitral rudimentary,	Recurrent mania.	Empyema.
19	M.	35	One flap of aortic valve rudimentary,	Chronic melancholia.	Acute nephritis.
22	M.	40	Aortic cusps fused together. Non-inflammatory,	General paralysis.	General paralysis.
24	F.	34	Two cusps to aortic valve,	Chronic melancholia.	Morbus cordis.
25	F.	38	Two cusps to aortic valve,	Acute mania.	
33	F.	57	Two posterior flaps to mitral, both rudimentary,	Chronic melancholia.	
36	M.	37	Two flaps to tricuspid, one large and one small,	General paralysis.	
37	F.	44	Four equal-sized cusps to pulmonary valve,	Chronic mania.	Mitral obstruction.
38	F.	54	Four equal-sized cusps to pulmonary valve,	Secondary dementia.	
44	M.	48	Four equal-sized cusps to pulmonary valve.	Secondary dementia.	
46	M.	75	Four cusps to pulmonary size,	Senile dementia.	
47	F.	69	One flap of mitral small a.	Secondary dementia.	

finally, the tricuspid is least often abnormal, being found to vary in 1 case only of either sex out of the 4252 examined.

Concerning the variety of the abnormality noticed, it will be observed that there are 5 instances out of the 20 cases in which there were only two cusps to the aortic valve, 3 of these occurring in males and 2 in females; this is therefore the most common site and variety of abnormality. Next in order comes redundancy of the pulmonary cusps, 4 examples of this being noticed out of the 20 cases, 2 in either sex, the valve segments being in three cases out of the four of equal size and symmetrical in shape, and in the fourth case one segment being much smaller than the others and greatly malformed. The third most common variety is to find one cusp of the mitral valve small and rudimentary, which occurred in 1 male and 2 females.

It has not been considered necessary to work out the percentages of occurrence of each of these abnormalities—all will be seen to be extremely rare—but an attempt has been made to demonstrate their relative frequency; and though some data on this subject may exist, the writer has been unable to find any such, either affecting the insane or the general community.

NOTE ON A CASE OF SIX LUMBAR VERTEBRÆ AND
ABNORMAL MIDDLE SACRAL ARTERY. By A. E.
TAYLOR, Downing College, Cambridge.

On exposing the posterior abdominal wall of an adult male, the aorta appeared to bifurcate higher than usual; on close investigation, however, it was found that the bifurcation took place in the usual situation (*viz.*, opposite the disk between the 4th and 5th lumbar vertebræ), and that the appearance of high bifurcation was due to the presence of a sixth lumbar vertebra below the bifurcation. An examination of the thorax showed that all twelve ribs were present, and it was therefore concluded that this sixth lumbar vertebra was sacral in origin, and had not fused with the other elements which generally go to make up the sacrum. An examination of the sacrum, however, showed it to be made up of five elements ankylosed together; and articulated to the post-axial end of this was the coccyx, consisting of four segments, with the faint trace of a fifth. At the pre-axial end the sacrum was joined to the sixth lumbar vertebra by ligaments and a large intervertebral disk. The costal and transverse processes were very wide, and moulded on the top of the sacrum, fitting closely to its upper surface, and bound by ligaments.

An examination of the lumbar, sacral, and coccygeal nerves showed that there was no rearrangement of the nerve cords corresponding with the alteration of the bony constituents of the pelvis.

The middle sacral artery was very large, giving off two lumbar arteries of the usual size, one on either side, to supply the parts corresponding to the fifth lumbar vertebra (each giving a branch into the spinal canal and a branch backwards, and a continuation into the muscles of the abdominal wall). It then proceeded, with gradually diminishing size, down the middle line to the tip of the coccyx. There was a very minute pair of lumbar arteries, also arising from the middle sacral at a lower level, and supplying the interval between the intercalated sixth lumbar vertebra and the first sacral.

CONTRIBUTIONS TO THE COMPARATIVE ANATOMY
OF THE NEUROGLIA:¹ BEING PART OF THE THESIS FOR
THE DEGREE OF DOCTOR OF MEDICINE OF EDINBURGH
UNIVERSITY, JULY 1897. By F. W. EURICH, M.D.
(PLATES XVI., XVII.)

To Golgi's method before all others is the honour due of having revealed to us, in their entirety, the units of which the nervous system is composed. It has sheared through the tangled mass of erroneous conceptions and contradictory theories, and has displayed the principles of nerve-architecture in all their beauty and simplicity. The neuroglia has shared with the purely nervous structures this beneficent influence. The neuroglia was shown to consist, in adult man, of masses of richly-branched cells—which Deiters had already, in part, seen—the branches constituting that intricate fibrous felt-work in which nerve-cells and nerve-fibres are embedded.

Two species of the glia-cells (syn., "astrocytes," "spider-cells") are recognised, each liable to slight variations according to the site they occupy. The first species, called "fibre-cells" by Andriezen, occur in both the white and the grey matter: they consist of a small, three- or more-sided body, with many long, smooth, wiry, generally unbranched processes issuing from it. These fibres may quit the cell-body from every part of its circumference, or only from one-half of it, as in the sub-pial layers, or merely from its two poles.

The second species of glia-cells is small, with short, branched, and rough processes, which are often so numerous as almost to hide the cell-body. Their habitat is almost solely the grey matter.

When Golgi's "rapid method" was applied to the embryonic nervous system, it was found that these glia-cells appear to develop from the ectodermic cells lining the central medullary

¹ In the course of these investigations we have been seriously handicapped by the impossibility of gaining access to much of the literature bearing on our subject. More particularly was this the case with the papers of Spanish and Italian authors: failing the original articles, we had to content ourselves with abstracts.

canal. This is now the generally accepted view, though it still finds an opponent in His; and Ramon y Cajal himself but a short time ago supported the dualistic theory of their development. It is possible to uphold such a dualistic theory, as not every stage from the ependyma-cell to the fully-formed astrocytes has as yet been observed in man. Nor can we supply the missing evidence, though we hope to furnish facts which will still further add to the probability that the ectodermic theory is the correct one.

It was soon found that in the lower vertebrates a similar developmental process to that in man took place. As embryo-rats and mice, and above all the chick, furnished material of a more manageable size and more readily obtainable in a fresh condition, the metamorphosis of the neuroglia was studied in these. Though this part of the subject has been very carefully worked out by Cajal and many others, we yet thought it desirable to study it from original preparations, partly because it forms the natural foundation for what is to follow, and partly because one or two points have not had attached to them that degree of importance which in our opinion they deserve.

The ependyma-cells, having sent each a long process to the periphery, begin to multiply till, not having sufficient room around the canal, they pass outwards. But before this passage outwards occurs, a bifurcation of the process takes place. Both bifurcation of the process and dislocation of the ependyma-cell begin in the ventral region of the spinal cord—excluding that small area which is destined to form, later on, the floor of the anterior median fissure. In other words, the bifurcation and the appearance of displaced ependyma-cells are first noticed in that part of the cord which, developing the fastest and curling over ventrally (thus forming the anterior median fissure), presents a greater increase in area, on transverse section, and an extent of circumference greatly surpassing that of the central canal. The importance of this is obvious. Assuming that the ependyma is intended to play a passive rôle—that is to say, either as a supporting or as an insulating agent to the nervous structures—it must do one of two things to fulfil its duties when the nervous structures grow and extend as above described: firstly, it may cause its long processes to divide, and thus cover a larger

field; and secondly, it may increase the number of its cell-elements and crowd them outwards; or it may do both. The first is chosen as the simpler alternative: after a time it proves insufficient, and is therefore combined with the other.

This explanation of well-known facts appears to us such a natural and important one, that we are surprised not to have come across it in the literature at our disposal. As the cord grows, the processes of more dorsally-situated cells become branched also, but never to such an extent as the ventral ones, which may give off three, nay, in some instances four branches, to the periphery. Not only the ependyma-cells at the central canal, but also those that have become displaced outwards present this bifurcation of their processes. We shall in future call these displaced ependyma-cells "astroblasts," following Lenhossek's example, and assuming them to be the progenitors of the "astrocytes." It may here be stated that, at or about the 8th day in the chick, shorter branches, not going to the periphery, are developed from the main processes of the anterior and lateral astroblasts at some spot between the point of bifurcation and the cell-body. These short branches, with few exceptions, pass directly forward; possibly their development may stand in some relation to those lateral neuroblasts which have at about this stage turned on their axes, so as to give their long diameter a sagittal direction.

Another salient feature of the ependyma-cells and their derivations, the astroblasts, is the gradual appearance of small and very delicate hairs and spicules upon the main process and its branches. Some observers have expressed a doubt whether these minute appendages are natural outgrowths or artefacts; but whatever opinion be held regarding them in adult man, we do not hesitate to pronounce them to be realities in the embryonic condition, and for the following reasons. They are not visible when the ependyma-cell is first seen: they appear first in the ventral, then in the lateral regions of the cord, and last of all in the posterior segments; they gradually increase in size in the same order in which they appeared, though they never in the dorsal regions attain to the same degree of development as in the ventral segments. Further, they vary in delicacy, in length, and in density of setting, according to the species of

animal examined. And lastly, as Ramon y Cajal had already observed, the fibre may retain or lose these appendages in its passage through different nervous areas. This is clearly shown in our preparations from the spinal cord of the chick at the 9th or 10th day, in which the hairs and spicules are lost as the fibre traverses the white matter. In other words, there appears to be a distinct relation between the appearance of the medullary sheath and the atrophy of these appendages. We shall have occasion to note the same circumstance in both the foetal and adult stages of other animals.

LEPTOCARDII; *Amphioxus lanceolatus*.—The spinal cord is phylogenetically the oldest portion of the central nervous system of vertebrates. It is found in its most rudimentary form in *Amphioxus* (F. Nansen), in which animal the ependyma-cells lining the central canal and their processes are the only representatives of the neuroglia. The cord has, on transverse section, somewhat the shape of a triangle, the base of which is situated ventrally, while the rounded apex constitutes the posterior extremity, into the very tip of which the central canal is prolonged. The canal does not, however, come so near the ventral surface, being separated from it by a huge unpaired nerve-fibre and a number of smaller ones. Corresponding to this development of the ventral half of the cord, the majority of the processes from the ependyma-cells have bifurcated in accordance with the principle mentioned above. Nansen's paper was, unfortunately, not accessible; and in such references to it which we were enabled to gather, no mention is made of the outline of the fibres: our own results, with the only two specimens of the animal obtained by us, are too imperfect to allow us to draw any conclusions.

CYCLOSTOMATA; *Petromyzon fluviatilis*.—We were not fortunate in our preparations from the cord of *Petromyzon* and its larval form, *Ammocoetes*. The loss, however, is not serious, for our knowledge of the neuroglia of the Cyclostomata is a very complete one, thanks to the labours of Nansen, Retzius and von Lenhossek. According to these observers, the ependyma-cells are scanty, each with a long, thin, smooth process going to the periphery, and often bifurcating near the edge of the grey matter. The rest of the supporting tissue is formed in *Myxine*, by true

astrocytes or spider-cells, which are almost confined to the grey matter, and send most of their numerous processes, generally branched, to the very surface of the cord. The individual elements send their processes either to the dorsal or to the ventral aspect, rarely to both. In the case of *Petromyzon* the same conditions are found, with this slight difference, that, as a rule, the astrocytes each distribute their branches to both ventral and dorsal surface. We would also point out that the branches of the more medially placed spider-cells cross the middle line in front and behind the central canal, and that we have here the first indication of that ring of neuroglia which is such a prominent feature around the central canal in man.

ELASMOBRANCHII.—The only author who appears to have studied the neuroglia in these fishes before us is v. Lenhossek. His material consisted of *Raja*, *Scyllium* and *Acanthias*. In *Raja* he found the ependyma-cells few in number, and possessing a delicate unbranched process, which passed to the periphery of the cord. The neuroglia-cells were in the form of astroblasts, with a solitary, strong, fluffy peripheral process reaching to the pia mater. In *Acanthias vulgaris* and in *Scyllium*, however, he succeeded in impregnating true astrocytes similar to those existing in *Petromyzon*, but not reaching quite to the surface of the cord,—appearing, instead, to end just beneath a sub-pial layer of ramifying dendritic nerve-cell processes. He failed to impregnate the ependyma.

Our own investigations dealt with embryos of *Raja*, 10 to 11 cm. in length, and with those of *Acanthias vulgaris*, measuring 13 to 14 cm., which were kindly supplied by the Marine Biological Station at Plymouth. The pieces were left in Golgi's solution of osmic acid and potassium bichromate for from sixty-four to ninety-four hours, at a temperature of the room, and were subsequently immersed for a period of forty-eight hours in a weaker mixture of the same, as recommended by Cajal, viz., 20 parts of a 3·5 per cent. solution of potassium bichromate, and 2 to 3 parts of a 1 per cent. solution of osmic acid. The best results were obtained when the pieces had been left in the first mixture for ninety-four hours.

1. *Raja* embryo, 10 to 11 cm. in length.—In this animal the neuroglia is in a comparatively primitive state, consisting, as it

does, solely of ependyma-cells and astroblasts, as v. Lenhossek has pointed out. The former have a small cell-body and a long elegant process passing up to the pia mater, where it ends in a small knob. This fibre is frequently branched—contrary to Lenhossek's statement—especially in the ventral part of the cord, where the division occurs well within the grey matter. The more dorsally distributed processes may also branch, but the bifurcation usually takes place just at the edge of the grey substance.

These fibrous prolongations of the ependyma are finely set with shorter or longer hairs, the latter often dividing like the processes themselves; and as no sharp distinction can be drawn between these two kinds of hairs, we may well agree with Kölliker, and look upon these hair-like appendages as the equivalents of processes. This hirsute character is, however, not a universal one: it is absent where the white matter is traversed, and it is wanting in those processes which form the ventral and dorsal median septa (except in the immediate vicinity of the cell-body in the case of the latter). A short branch, passing directly backwards, which may or may not divide, arises close to the body of one or two lateral ependyma-cells. The astroblasts share the general characters of the ependyma as regards the bifurcation and the hairiness of their processes: they may, in addition, despatch a process of varying length in the direction of the central canal. Astroblasts can be found throughout the grey substance up to its junction with the white matter, but are most numerous in the interior. We were unable to discover any within the white columns.

Some of the astroblasts call for special notice. Those that lie at the outer edge of the grey matter may change their originally radial direction for one approximately parallel to that edge, and may send two processes to the pia mater, one from each pole. Very pronounced examples of such cells may be found in the grey matter abutting on the posterior extremity of the anterior white columns, of which cells one process passes to the pia through the anterior horn, the other by way of the ventral septum; and it is worthy of note, that while the former process is well clothed with hairs as it traverses the horn, the other process is naked in its course within the septum.

Secondary processes, springing from the body of the cell itself, are common in astroblasts near the white columns.

Another variety of the astroblast, to which we wish to draw attention, lies close to the central canal. It, too, has abandoned its radial position, and has adopted a more or less sagittal one, so that its two processes pass forwards and backwards respectively: the former either takes part in the formation of the ventral septum, or enters the anterior horn of grey matter, there to end apparently; the latter usually bifurcates, and sends at least one of its divisions across the middle line behind the central canal. It will thus be seen that here again we have an early indication of Stilling's "ring-commissure." To summarise: we find in *Raja*—i. Ependyma-cells, delicate, often branched, hirsute, but smooth in white matter. ii. Astroblasts throughout the grey matter, and resembling the ependyma. iii. Early indication of a "ring-commissure." iv. No true astrocytes.

2. *Acanthias vulgaris*: Embryo 13–14 cm. (see Plate XVI., figs. 1 and 2).—In this animal, in the spinal cord of which Lenhossek succeeded in staining only true astrocytes, we were able to impregnate all three varieties of neuroglia elements—the ependyma-cells, the astroblasts, and the astrocytes. i. The ependyma does not differ markedly from that found in *Raja*: the main processes are well developed, pass to the very periphery of the cord, often branching, particularly in the antero-lateral regions, are finely hirsute, and tend to become smooth in the white matter. Particularly does this appear to be the case in the anterior columns, while laterally the white matter contains many dendritic ramifications of protoplasmic nerve-processes, and is traversed not only by smooth but also by roughened neuroglia fibres. As a matter of fact, even the anterior tracts are not *quite* free from the naked branches of nerve-cells, and, in accordance with this, contain a few hirsute fibres. The ependyma processes forming the ventral and dorsal septa are smooth, as in *Raja*, save that one or two in the ventral septum may be found possessed of minute and scanty spicules.

ii. The astroblasts show a distinct advance on those found in *Raja*, being placed not only in the grey, but also in the white matter, where they are more numerous in the anterior than in the lateral tracts, and more numerous in the lateral tracts than

near the posterior horn. Golgi's method is, of course, unreliable in questions of quantitative distribution, but sections treated with any nuclear stain clearly demonstrate the above conditions. Astroblasts which have changed their radial position to one more or less tangential to the outer edge of the grey matter are also seen, likewise cells which send out secondary processes. As in Raja, so here, one or two astroblasts have assumed, close to the central canal, an antero-posterior direction, some pushing their processes across the middle line behind the canal. But this primitive "ring-commissure" is strengthened by branches from the third class of neuroglia-elements—the astrocytes proper.

iii. These cells appear to have a large body, from which a varying number of fibres, five to ten, often branched, arise. The majority of these processes are smooth, but examples are not rare upon which fine hairy appendages are more or less richly distributed: frequently only one of the branches is thus distinguished. The fibres are often of great length, reaching, it may be, from one anterior horn to the other, or from an anterior horn far into the posterior grey substance. We were able to follow some of these fibres up to the pia mater, but the greater number of them appear to end short of the periphery, as Lenhossek described them. The astrocytes are practically confined to the inner regions of the grey matter, only some few stray specimens being visible in the horns proper. One such cell we found in an anterior tract of white matter; another, seemingly in the white matter just dorsal to the postero-external tip of the anterior horn; but as it is very difficult, if not impossible, to define the limits of the grey matter, the latter cell may well have been within it. Astrocytes from nearly all parts of the grey matter send branches across the middle line in front and behind the canal, thus forming, together with branches of astroblasts, as above mentioned, a perfect felt-work around the central canal. Of special interest are cells which appear to represent transition-forms from the astroblast to the astrocyte. We have figured such a cell in the posterior grey matter: it sends a large straight, smooth, bifurcated process to the periphery, while a number of long delicate branches radiate through the grey matter in all directions. Another cell of very mixed character

is represented at the junction of the left anterior horn with the posterior grey matter. A third cell, with all the features of the astrocyte, was found sending a process up to the "membrana limitans interna" of the central canal. In conclusion, we must remark that astrocytes sometimes present a peculiar appearance, as though their fibres did not really spring from the cell body, but were merely placed in apposition to it. We were, however, unable to satisfy ourselves that this was really the case: were it so, then it would furnish a parallel instance to what Andriezen has noted in man.

To sum up, the spinal cord of *Acanthias vulgaris* possesses—
 i. Ependyma-cells, as in *Raja*. ii. Astroblasts, in white as well as in grey matter. iii. True astrocytes, and also transitional forms. iv. A "ring-commissure," formed by branches of astroblasts and astrocytes.

The cerebral cortex, both of *Raja* and *Acanthias*, appears to contain only ependyma-elements, possessing all the characters of those found in the spinal cord.

TELEOSTEI; *Gadus luscus*, etc. (see Plate XVI, figs. 3 and 4).
 —Retzius appears to be the only one who has, up to the present, published any results from observations on the fully formed neuroglia in these fishes. But even his researches appear to have been confined to young animals. He only succeeded in finding ependyma-cells and astroblasts, very rough and furred. The genus *Gadus* furnished us with the necessary material. The neuroglia in these animals is a complex tissue, presenting cells of several types and many transition forms, so that a better idea can perhaps be obtained from the plates than from any verbal description that we can give. Beginning with the ependyma:—
 i. We find the cell bodies small, and the fibres fairly strong and hirsute, but apparently somewhat atrophic, and not reaching to the periphery save in the ventral septum. Whether the ependyma fibres of the posterior septum also reach the pia we were not able to determine: certain it is that branches from astroblasts and astrocyte-like cells within the posterior grey matter contribute largely to it. The ependyma fibres of the two septa are hirsute for only a short distance from the cell-body.

ii. Astroblasts abound in both grey horns. They possess a

hairy main process which is sometimes bifid, which probably in all instances reaches to the pia, and which loses its roughnesses as it traverses the white columns. They also exhibit secondary offshoots from the cell-body, which offshoots may be short and stubby, or of some length, especially in the case of the more externally-situated elements, and may be partially hirsute or perfectly smooth. These same secondary branches occasionally encircle blood-vessels. A few astroblasts are also found in the white matter, particularly in the lateral columns, where they tend to lie in bundles and thus form trabeculae. At the edges of the anterior horns they betray more of the characters of the astrocytes and show some rotation, assuming a more tangential direction. In the more dorsal parts of the posterior horn many of the astroblasts which lie nearest the septum display a degree of ramification of the principal process as in no other locality within the cord; but it must not be forgotten that these are in all probability not astroblasts in the strictest sense of the term—i.e., ependyma-cells pushed outwards by multiplication—but original ependyma-cells displaced by the fusion of the walls of the central canal behind; their processes do not appear to reach the periphery.

iii. The third type of neuroglia-elements—the astrocyte—is present in both the varieties mentioned in the introduction—viz., the smooth, long-armed, wiry-looking “fibre-cell,” and the furred, short-armed species. The former variety predominates. The “fibre-cell” may be found sparsely scattered in the white matter: its chief site, however, is the grey matter, especially the region of the central canal and the anterior horns; to a lesser degree, the sides of the posterior septum, which septum they assist in forming. The cell-body is sometimes triangular, often flat and disc-like, and appearing to lie in apposition to the fibres. These fibres, or branches, do not radiate in all directions, but in somewhat of a bipolar fashion, dividing as they go. This variety of astrocyte is the principal factor in the formation of the ring-commissure, though the secondary branches of astroblasts also take part in it. Of most of the glia-elements within the white substance, it is difficult to determine whether they should be called “astrocytes” or “astroblasts,” and are, perhaps, best considered as transition

forms. "Fibre-cells" here and there come in contact with vessels: these they sometimes partially encircle, sometimes they pass along them, strengthening their adventitia. The fibre-cells and transition forms found in the white matter sometimes join to help in the formation of the trabeculae above mentioned, the fibres of which may occasionally be seen passing for some distance just beneath the pia along the surface of the cord.

The second, short-armed variety of astrocyte we found in the grey matter only, and there confined to the body of the anterior horns and to the dorsal half of the posterior mass of grey matter. In the latter locality they appeared rougher than in the anterior horns, and perhaps a little more branched. Nowhere could we detect any relation to blood-vessels, but we would not like to deny the existence of such a relation, as our preparations were not very satisfactory in this respect. Once or twice we noticed elements which might be looked upon as transition forms from the astroblast to this species of astrocyte: two such cells have been figured in the left anterior horn.

Summarising, therefore, we may say, that in the teleostean cord the three species of glia-elements are found: i. the ependyma-cells, atrophic; ii. the astroblasts; and iii. two types of astrocytes (not one type, as in *Acanthias*). Transition forms between ii. and iii. occur; and the "ring-commissure" is more fully developed. Some astrocytes enter into relation with blood-vessels.

Sections from the optic lobes and from the cerebral hemispheres unfortunately disappointed us.

AMPHIBIANS.

ECAUDATA; *The Frog (Rana temporaria)*.—The neuroglia of the spinal cord of the frog has been studied by several observers, especially by Lavdowsky and Cl. Sala y Pons. Quotations from and abstracts of the work of these men were alone available; but what we have been able to gather in this way has, on the whole, served us well. Both men agree in describing the neuroglia as being remarkably primitive, even in the full-grown animal; but while Sala y Pons could only find ependyma-cells and their direct derivatives, the astroblasts, Lavdowsky described

and figured delicate glial elements in the white matter, with all the characteristics of true astrocytes. Both Lenhossek and Kölliker were unable to verify this statement, and Lavdowsky so far stands alone. Lenhossek and Kölliker are, however, not inclined to dispute the correctness of Lavdowsky's observations, as they have seen "undoubted glial nuclei" among the white columns, with the help of other methods. We, too, have met with no better success, and rather incline to the belief, after very careful examination, that the nuclei which can be seen with stains, such as hæmatoxylin or van Giesen's, are *not* neuroglial in nature, but leucocytes; they have all the characters of the white cells, as seen in the blood-vessels, and are, moreover, also found in the optic lobes and in the cerebrum, where astrocytes are known *not* to occur, as will be shown later. It would be anomalous, according to our experience, to find true smooth-fibred spider-cells in the white matter, and a very primitive form of the astroblast in the grey; for we have hitherto found that in the lower vertebrates, astrocytes appear first in the grey matter, with a special predilection for the region round the central canal. What Lavdowsky may have mistaken for spider-cells we cannot conjecture, but it certainly is strange that three men, Sala y Pons, Lenhossek, and Kölliker, so well practised in Golgi's method, should have failed to stain a structure which, in other animals than the frog, is not one of the most difficult to impregnate. Be that as it may, the neuroglial elements which *all* investigators have succeeded in demonstrating, present somewhat primitive shapes. They consist solely of ependyma-cells and astroblasts. Both kinds of cells possess a strong, stiff, and very hairy principal process, passing to the pia mater, but the ependyma fibres, forming the posterior system, are smooth. Branching appears to be the rule, with few exceptions; the division occurring well within the grey matter. Within the white matter the neuroglia fibres become smooth, and, as they approach the pia, swell into a conical extremity, thus giving the impression, on hurried examination, that they have sprung from cells just beneath the pia, if the section should happen to have severed the connection with their cell. The nakedness of the fibre is best marked anteriorly; for in the lateral columns, which contain a large number of dendritic nerve-cell processes, a

moderate hirsute appearance is still noticeable on many. Very short secondary processes are given off by the bodies of the astroblasts, while here and there a short lateral offshoot arises from the main fibre. Astroblasts are found in every part of the grey matter: where it joins the white substance, the elements tend to turn on their axes, so as to give their main processes at first somewhat of a sagittal direction. Such boundary-cells often possess, not one, but two, or sometimes three processes, of relatively equal importance, each of which may bifurcate; at other times there is a principal process, which, after a very short course, breaks up, candelabra-like, into three or four divisions. The astroblasts in the posterior horn have more tortuous processes than the rest, reminding of the S-shaped fibres found in the same situation in the embryos of higher vertebrates. There is no trace of a "ring-commissure"; the only crossing of neuroglia fibres, and a very scanty one, occurs in front of the canal, and is composed of one or two secondary processes from adjacent astroblasts, aided in the rare event of a neighbouring ependyma fibre passing into the opposite hemisphere. A few ependyma fibres appear atrophic (?).

The neuroglia of the optic lobes and of the cerebrum is soon described. In the optic lobes it is represented by ependyma-cells only. Each cell sends a long, perhaps wavy, delicate, and generally slightly branched process to the periphery. This process also gives off a number of small, lateral twigs, and is richly set with hairs. It has seemed to us as though the branching of these fibres was most pronounced in the lateral regions of the lobes. Not all the ependyma-cells directly line the optic ventricle; some are pushed a little distance outwards, but still remain in contact with the ventricular wall by means of a short thick process which passes up to the lumen. In the cerebral cortex the condition is practically identical, save that all the ependyma-cells directly line the lumen of the ventricles, that the main processes are a trifle more wavy, and that branching occurs much nearer the cell-body than in the optic lobes.

Summary.—i. Ependyma fibres thick, branched, hairy; sometimes apparently atrophic. ii. Astroblasts with all the characters of ependyma-cells. iii. No ring-commissure. In the optic lobes and the cerebral cortex, there is only ependyma.

BIRDS.

The Pigeon ; Columba (see Plate XVI., figs. 5 and 6).—Carefully and minutely as the neuroglia has been studied in the embryo chick, it has been as strangely neglected in the case of the adult bird. Kölliker confines himself to the statement that the cerebrum of birds contains not only ependyma, but also (somewhat vaguely) “true glia-cells,” and omits all reference to the spinal cord. Weigert, giving Sala y Pons as his authority, says that the spinal cord contains spider-cells, and the cerebral cortex only transition forms. Lenhossek, though apparently acquainted with the work of Sala y Pons, which appeared a year before his own, betrays no knowledge of these facts, and roundly states that investigations on the adult avian neuroglia are still a desideratum. He subsequently says that in the embryo chick at the 15th day he succeeded in impregnating what he believed to be true astrocytes, but hastens to add that his preparations are not altogether convincing. Sala y Pons’ monograph itself was unfortunately beyond our reach.

Our own investigations were made upon the nervous system of *Columba*. The mode of treatment was similar to that adopted in the previous cases, the pieces remaining from four to six days in Golgi’s solution, a sojourn of six days giving perhaps the best results. We further found it advisable to clear the sections completely before deciding upon their rejection or preservation; instead of examining them as soon as cut, which is the usual practice: this was found to be of special utility in the case of the spinal cord, where, unless the above precaution has been taken, the delicate neuroglia-elements are very difficult to discern between the darkly-stained medullated fibres of the white matter. Many sections which would, under ordinary circumstances, have been rejected as valueless, were thus found eminently useful.

In the spinal cord we found two distinct classes of neuroglia-element present—ependyma-cells and true astrocytes, together with a sub-variety advanced beyond the ordinary type of astroblast, yet below that of the true spider-cell.

i. Ependyma-cells were found impregnated at every point of

the circumference of the central canal, but their processes could not be followed to any distance, appearing as smooth, evidently atrophied, fibres. These fibres were best preserved in the two septa, ventral and dorsal: in the former they reached the floor of the anterior median fissure in a few instances; posteriorly they could be followed a considerable way to the periphery, but whether they actually reached it could not be determined. The question whether the posterior septum contains ependymal fibres in its whole extent, or whether its most peripheral portion is solely composed of branches from adjacent glial elements, is thus left open.

ii. Astrocytes or spider-cells are to be found both in the grey and in the white matter, and present two well-pronounced types—a long-armed, and a short-armed variety. The cells of the first type have a small stellate or triangular or sometimes disc-like body, from which a varying number of branches (seven to twelve, or more) radiate. These offshoots are long, delicate, smooth, peculiarly stiff in appearance, and frequently branched; they may arise from every part of the cell equally, or they may be restricted to the two poles, or they may leave one side of the cell bare. These astrocytes are most distinctly stellate in the centre of the anterior horns, and in the middle of the anterior and lateral tracts of white matter. Within the grey substances they are found in greatest profusion in the neighbourhood of the central canal. The cells nearest the ependyma are placed more or less sagittally, and have somewhat of a bipolar character, their fibres passing forward and backwards, and diverging in a brush-like fashion, so that many cross the middle line in front and behind the canal. The farther the cells are from the canal the more stellate or spider-like do they become; still, however, sending branches to assist in forming the “ring-commissure.” It will be noticed that this structure is here found to consist, for the first time, of fully developed astrocytes only. The spider-cells in the anterior and lateral columns of white matter require little description. As we stated, their stellate character is best preserved in the centre of these columns: the more they approach either the grey matter or the pia mater, the more do they vary their shape. Thus, near the anterior horns they frequently send a couple of processes longer than the rest into

its substance, where they may form attachments to vessels. As the cells approach the pia, on the other hand, their processes to the periphery naturally shorten, often appear a little thicker than the rest, and allow the branches to the interior to predominate. This shortening of the peripheral fibres is in some cases more apparent than real, in which they spread out beneath the pia, passing in opposite directions along the surface of the cord. Besides these smooth, long-armed astrocytes, a second type is met with, practically confined to the grey matter beyond the "ring-commissure." These cells have all the characteristics of the short-armed variety described at the beginning of this paper: they possess a very small body, giving off an immense number of short-branched, "frosted" processes. This class of cell is perhaps best seen at the junction of the anterior and posterior horns, and in the neck of the latter. Very frequently this type of cell possesses in addition one, two, or even three processes considerably longer than the rest, slightly wavy in their course, not quite so richly set with hairs (sometimes even smooth), and generally attached to a blood-vessel. This latter variety of cell is so common that a doubt whether in the former the longer process has not been lopped off in cutting the section appears almost justified. Transition forms between the two extreme types of astrocytes—the long-armed, spider-cells characteristic of the white matter, and the rough, bushy, short-armed elements—are easily discernible, especially where grey matter and white matter meet.

Still another variety of the glial elements requires description. It is found in the "cap" of the posterior horn, in a narrow strip of white matter bounding it externally, and in an area corresponding to Lissauer's tract and the entrance of the posterior nerve-roots. These cells have all the appearances of the old astroblasts—the long peripheral fibre, smooth in the white matter, hirsute in the grey, and very rarely bifurcating, together with the short secondary processes springing from the cell-body, also set with fine hairs when passing through grey substance. These cells, too, contain transition forms, viz., in the direction both of the long-armed and of the short-armed class of astrocytes: thus, one or two of the secondary processes may attach themselves to vessels, or they may lengthen, and, losing their hair:

like appendages, penetrate as smooth fibres for some distance into grey or white matter.

A word or two concerning the relation of the glia-elements to vessels, which had already been noted in the Teleosteans. Both long- and short-armed astrocytes show this relation in birds. The branches of the latter variety attach themselves immediately to the vessel-wall; the branches of the "fibre-cell" may do likewise, but they may also accompany the vessel for some distance, thus strengthening the adventitia. They do not appear to pass along a vessel in the oblique direction of a long spiral, as Andriezen describes in the case of man.

In the cerebral cortex the glial elements are of a much simpler description. The ependyma-cells are delicate, and their fibres are still in good condition, appearing to reach to the periphery, though their roughness has somewhat diminished. The other elements of the neuroglia have not passed beyond the stage of the astroblast, but can be found in all regions and layers of the cortex. Their bodies are small, but their main process strong and fluffy, somewhat tortuous in the outer strata, and sometimes branching. The nearer the cell approaches to the pia, the more do small secondary processes develop, till just beneath that membrane an appearance is presented very like that of the short-armed astrocyte in the cord, but lacking its elegance, due to an approximation of the length of the main fibre to that of the secondary cell processes. The hirsute condition of the fibres appears greatest in the outer layers of the cortex.

In the optic lobes the same conditions prevail, save that the fibres are smoother generally, and that their roughness is perhaps most marked near the ependyma, and *not* near the periphery, as in the cerebral cortex. This difference is possibly in part due to differences in the arrangement of the medullated fibres in these two regions. Neither in the cerebral cortex nor in the optic lobes did we find any trace of glia-elements in a more advanced stage of development.

Summary.—A. In the spinal cord we have found:—i. Atrophic ependyma fibres; ii. glia-elements the shape of astroblasts in the posterior horns, and at the entrance of the posterior roots; with transition forms in the direction of—iii. the astrocytes. These presented two varieties: (a) the long-armed type in white

and grey matter, and forming a "ring-commissure"; (β) the short-armed, bushy astrocytes. iv. Transition forms between these two kinds of astrocytes. v. Well-marked relation to blood-vessels.

B. In the optic lobes and the cerebral cortex we have found—i. ependyma-cells with fully-formed fibres; ii. astroblasts in all layers, but approaching in character to the short-armed astrocytes in the superficial, sub-pial layers.

HIGHER MAMMALIA.

The structures of the adult mammalian neuroglia need not detain us long. Its elements have been briefly described at the beginning of this paper, and all important details can be found in any modern text-book of anatomy. It will suffice to state—i. that the ependyma fibres, though present, are atrophic, save, perhaps, in the anterior and posterior septa; ii. astroblasts appear to be absent; iii. astrocytes constitute practically the whole of the neuroglia, and are present in the two varieties—the "fibre-cells" and the short-armed spider-cells—the latter being practically confined to the grey matter; iv. the fibre-cells, besides forming a dense "ring-commissure" around the central canal (and the ventricles), invest the whole of the central nervous system (with very few exceptions) with a sub-pial felt-work of varying thickness, which felt-work accompanies the blood-vessels into the interior of the nervous organs in the shape of trabeculae; v. the short-armed variety of astrocytes may still present in very late embryonic life a long main process—which has been seen to be a permanent condition in birds; vi. at the edge of the grey matter of the cord long fibre-cells can be seen, almost bipolar in character, sending their fibres along the outer edge of the grey substances—thus reminding us of somewhat similar cells seen in Raja, Acanthias and Rana; vii. both types of astrocytes frequently show an intimate relation to blood-vessels, either attaching themselves to them as soon as reached, or passing along them in an oblique direction; viii. no true connective-tissue enters the nervous organs except the little that is imported by the vessels.

Having now come to the end of our results, obtained with

Golgi's method, as far as time and material permitted us, it may be well to dwell awhile on these results, and to summarise the conclusions that we have arrived at. To avoid prolixity, we put them in the form of propositions, as follows:—

1. The neuroglia, using the term in its widest sense, presents itself in various stages of its evolution in the various classes and orders of vertebrates, from the condition of a simple ependyma (as in the cord of *Amphioxus*) to that of the astrocyte (as in birds and mammals), which evolution is reflected in the embryos of the higher forms of vertebrates.

2. This process is exemplified not only in the different classes and orders, but also in different parts of the nervous system of one and the same species, *i.e.*, phylogenetically.

3. These phylogenetic differences are manifest not only in the larger divisions of the central nervous system, such as the spinal cord and the cerebral hemispheres, but also in the more minute topographical divisions of the various nerve-centres; *e.g.*, in the spinal cord of the pigeon, elements of a more primitive character are to be found in the cap of the posterior horn, and at the entrance of the posterior nerve-roots, than elsewhere in the cord; or, again, forms of a more advanced type may be found in the grey matter, and especially in the neighbourhood of the central canal, as in *Petromyzon*, *Myxine* and *Acanthias*.

4. Transition forms between the lowest and the highest types of neuroglial elements are met with, temporarily in embryos, or permanently in the adult animal.

5. In whatever stage the neuroglia may present itself, it always gives the impression of playing a *passive* rôle in the economy of the nervous system.

6. In other words, the mode of its development and evolution is capable of a similar interpretation.

7. From this point of view, the fibre, with its branches, would be the more important part of a glial element. It would appear that, as the area "supplied" by a fibre expands, that fibre will give off branches to meet such increase of area. A similar end is attained by the multiplication of the cells themselves, and by their passage outwards into the nervous tissue, which change in position widens the base of operation. The more the extent of this base-line approaches that of the circumference of the area

to be "supplied," the more easily can the fibres play their part; *a fortiori*, if the cells, from which the fibres spring, have reached the circumference of the area to be supplied, and can send their fibres inwards. Every cell which has passed away from the central canal has obtained this advantage over the area of nervous structures between itself and the canal.

8. The passive rôle which the neuroglia may play is either that of a supporting and protecting tissue, or that of an insulator, or both, for it is difficult, if not impossible, to decide upon one to the exclusion of the other. The theory that it is an insulator has been strongly advocated by the brothers P. and S. Ramon y Cajal and by Sala y Pons: they based it upon the apparently richer development of the neuroglia in the white matter than in the grey, as shown by Golgi's method. Weigert, however, has demonstrated that this method is by no means a safe guide in a question of quantitative distribution, and has shown that the grey matter is, in fact, the richer of the two. This correction as to fact would not, however, appear to us to affect the theory. What necessity, we ask, is there for such an insulator in the white substance when the medullary sheath in all probability already serves that purpose? But in the grey matter things are different: here axis-cylinder processes and their collaterals break up into an immense number of naked terminal ramifications, which interlace with each other and around the nerve-cells. Here an insulator is obviously needed, and the neuroglia may well serve this end.

9. As a further argument in favour of Sala's theory, the following may be put forward. The smoothness of a neuroglia-fibre appears to stand in some relation to the presence of medullated nerve-fibres in the regions traversed by that fibre, *e.g.*, the antero-lateral columns. But if naked axis-cylinders or protoplasmic processes of nerve-cells become mingled with the medullated fibres, then rough and smooth glia-fibres may coexist in that region. Hence we may suppose that neuroglia-fibres at one stage of their life-history fulfil a function that is afterwards undertaken by the medullary sheaths, and that on the development of the latter they are relegated to the inferior, but still important, office of a supporting tissue.

10. Regarding the "ring-commissure," the substantia gelatinosa

centralis and its homologues around the ventricles, etc., occupy the region which formed the first bed of the neuroblasts and early nerve-cells. This bed was vacated in the course of development, but the supporting tissue remained, and the vacated site became filled with neuroglia. The substantia gelatinosa centralis may hence, we think, be looked upon as a natural cicatrix, if such a term be admissible. The extent of development of this ring-commissure is an index of the age (phylogenetically considered) of the organ.

The mode of formation of the sub-pial felt-work, and the question as to the spontaneous movement of glia-cells, have found brief consideration elsewhere.¹

EXPLANATION OF PLATES XVI., XVII.

Fig. 1.—Spinal cord of *Acanthias vulgaris* (embryo), showing ependyma-cells and astroblasts, and a few transition forms. *a* = anterior, *b* = posterior septum.

Fig. 2.—Spinal cord of *Acanthias vulgaris* (embryo), showing astrocytes. Letters as before.

Fig. 3.—Spinal cord of *Gadus morrhua* and *G. luscus* (adult), showing ependyma, astroblasts, and astrocytes. Letters as before. *c* = Mauthner's fibre.

Fig. 4.—Spinal cord of *Gadus morrhua* and *G. luscus* (adult), showing the region of the central canal and ring-commissure. Edge of grey matter in this, as in all other sections, red. Letters as before.

Fig. 5.—Spinal cord of pigeon (adult). *a* = anterior median fissure; *b* = posterior septum.

Fig. 6.—Spinal cord of pigeon, showing region round central canal. Letters as before.

All the drawings have been constructed by synthesis. For a fuller description of the plates, see text.

¹ *Brain*, 1897. Winter number—"Studies on the Neuroglia.—II."

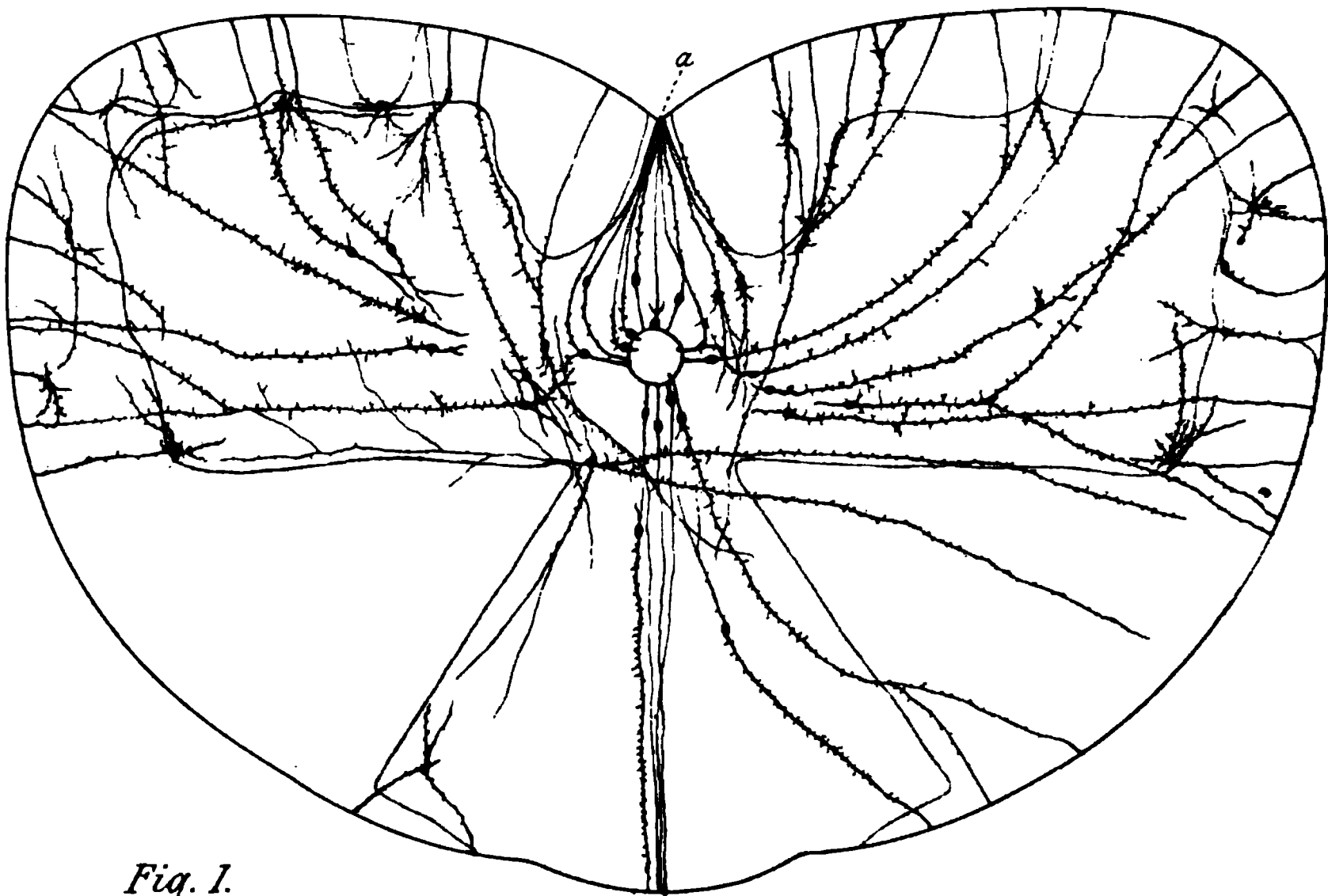


Fig. 1.

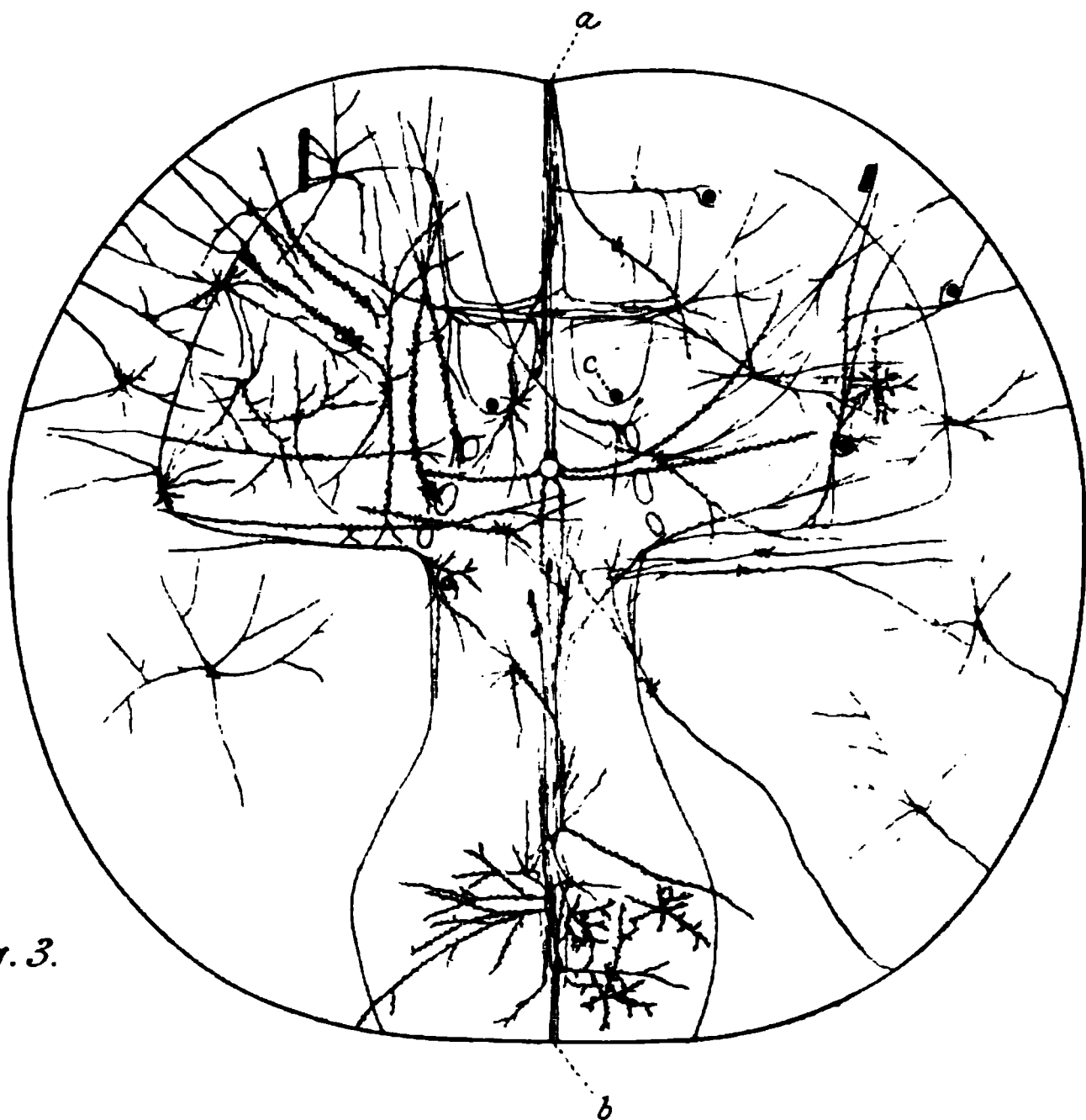


Fig. 3.

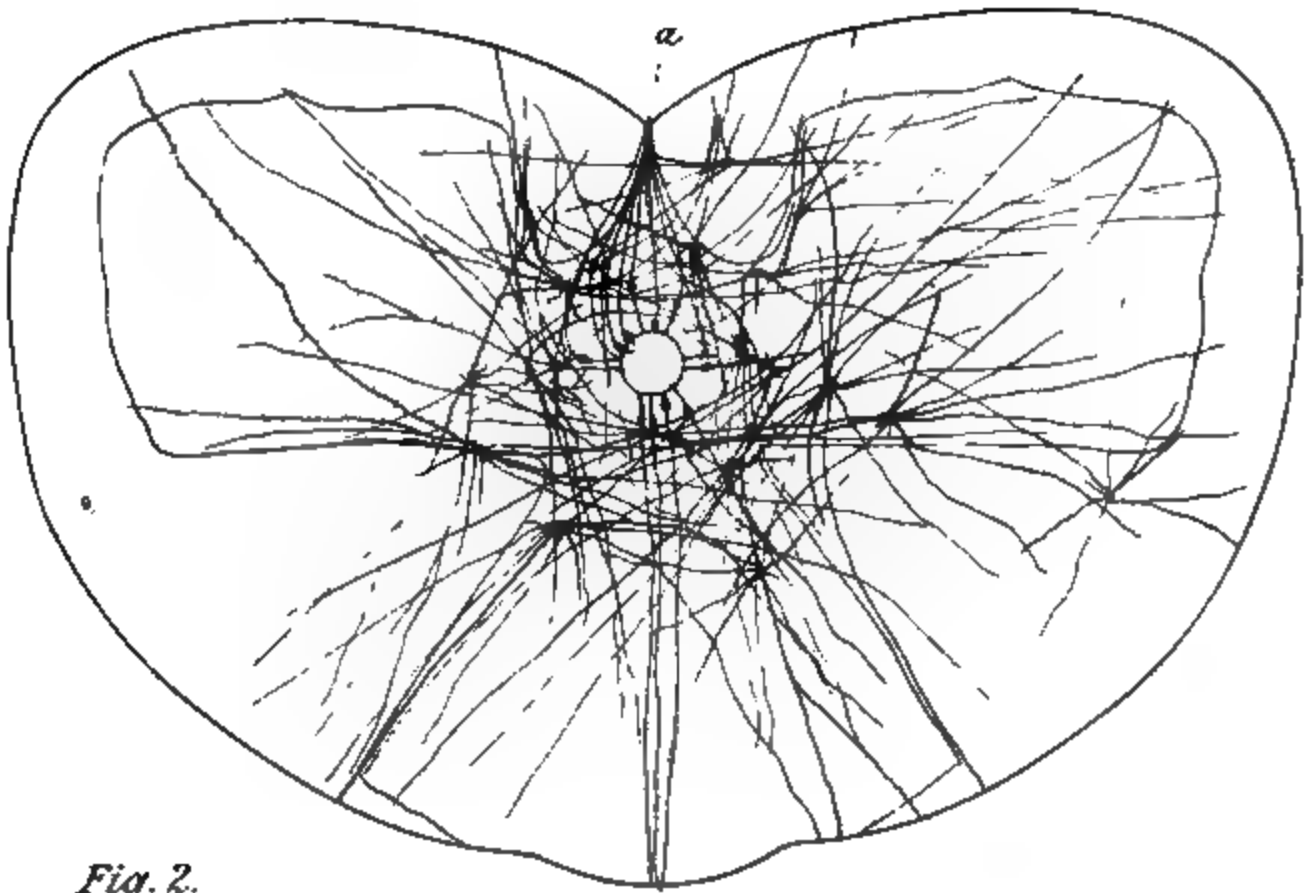


Fig. 2.

b
a

Fig.

b

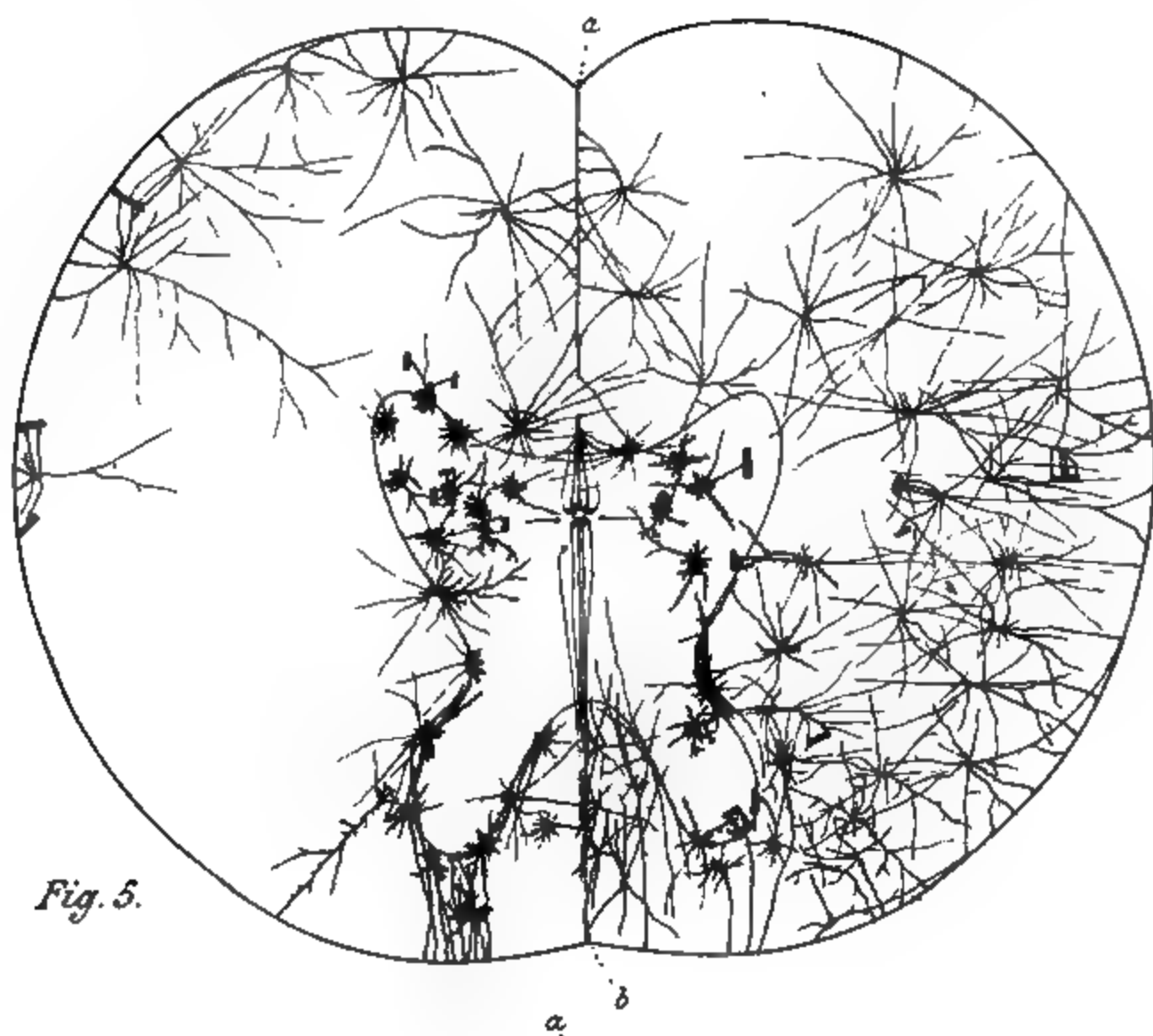


Fig. 5.

Fl

ON THE ORGAN OF JACOBSON IN THE HYRAX.
By R. BROOM, M.D., B.Sc., Namaqualand. (PLATE XVIII.)

FROM my researches among marsupials and other mammals, I have been deeply impressed with the importance of the structure and relations of Jacobson's organ as a factor in classification, and one which, from its constancy even under the most varied conditions of life, is probably one of the most valuable in determining the affinities of any obscure animal or group. Having already studied the organ and its relations in most of the mammalian orders, I was naturally very anxious to examine the condition in the Hyrax, as an examination would probably throw additional light on the affinities of this remarkable form, which, notwithstanding the many points in which it resembles the ungulates, and the marvellous agreement of the molars with those of the rhinoceros, has, it must be admitted, certain cranial characters, apart altogether from the superficial resemblance in the upper incisors, in which it agrees apparently more with the rodents. As the organ of Jacobson is in all rodents that have yet been examined constructed on a type quite dissimilar to that in the ungulates, it seemed likely that the study would at least determine whether there was any real affinity between the Hyrax and the rodents.

I am unfortunately unable to give the species of the Hyrax examined. Thomas limits the western range of *Procavia capensis* to the neighbourhood of Cape Town, but a species is found not only right through Namaqualand, but also, I am led to believe, on into Damaraland. Though the species is apparently closely allied to *P. capensis*, it differs in having only twenty-one ribs. As it is unlikely, however, that any perceptible difference will be met with in the organ of Jacobson in the various species of *Procavia*, the exact species of the Hyrax examined is not of much importance for the present purpose.

Apart from the condition of the organ of Jacobson, there are a number of points in the anatomy of the snout in which the Hyrax departs considerably from the more usual mammalian type. The transverse ridges of the palate are very well developed, and in the anterior part, and just behind the larger incisors, there is found a very large rounded pad of connective tissue, very much resembling in appearance the large papilla of the wombat and other marsupials; but though probably similar in function, it is not a true homologue, as there is a minuter true papilla further forward. This large false papilla is supported by a small downward process from the well-developed palatine process of the premaxillary. In no other mammal that I am aware of is a similar development found, though the prevomer in *Gomphognathus* has a median downward development which is strikingly like this structure in the Hyrax.

When the organ of Jacobson is examined, the condition is found to be exceedingly interesting, and in some respects different from that of any other mammal as yet examined. As would be inferred from the well-formed palatine processes of the premaxillary, the cartilages of Jacobson's organ are well developed; and though the organ is less developed than the cartilages, it extends to a little beyond the posterior end of the palatine process. Owing to the somewhat complicated condition of the cartilages in the anterior region, it will be more convenient to describe the organ from behind forwards.

Fig. 1, Plate XXII., represents a section in the transverse plane passing a little behind the posterior border of the anterior palatine foramina, and shows the condition and relations of the most developed part of the organ. In the outer side of the well-developed palatine process (*p.Pmx.*) lies the cartilage of Jacobson—irregularly U-shaped. It rests on the palatine plate of the maxillary, and is remarkable chiefly for its having attached to its outer and lower corner the posterior development of the outer nasal-floor cartilage (*o.n.f.c.*). In a number of very dissimilar types, such as in *Echidna*, *Lepus*, *Miniopterus*, etc., this outer nasal-floor cartilage is well developed posteriorly; but I am not aware of any other form in which it becomes completely united to Jacobson's cartilage, although in *Echidna* the elements are practically in contact.

A little behind this plane the outer nasal-floor cartilage is lost, and Jacobson's cartilage has on section the usual C- or U-shaped appearance. The organ itself is less developed than in most of the lower mammals, and resembles in its structure that of the ungulates much more than that in the rodents. It receives along its upper edge the ducts of numerous glands; and on its outer side, within the cartilaginous sheath, is a very irregular plexus of veins.

Fig. 2 represents a section near the middle of the anterior palatine foramen. Here, the outer and inner walls of Jacobson's cartilage are closely approximated above, and form almost a complete tube for the duct of the organ. The outer nasal-floor cartilage is more developed than in the posterior sections, but still, as in these, forms with the premaxillary a complete floor to the nasal cavity. On this plane the organ is represented by the posterior part of its long duct, which is on section somewhat rounded, and lined with columnar epithelium. There is still here, as indeed there is, up to where Jacobson's duct opens into the naso-palatine canal, a number of larger veins in close relationship to the duct.

In fig. 3, which illustrates a slightly oblique section near the anterior border of the anterior palatine foramen, we have on the left side Jacobson's cartilage passing up by the side of the palatine process to unite with the nasal septum. Towards the lower part of the palatine process the cartilage curves inward and below it, and forms a very deep channel for the lodgment of the duct of the organ. The outer nasal-floor cartilage is still attached to the lower part of Jacobson's cartilage. On the right side of the figure, which is a little in front of the other, the premaxillary is about to unite with its palatine process, and in the angle between the two bony structures lies the upper part of Jacobson's cartilage,—united above to both the inner part of the nasal-floor cartilage proper, which rests on the palatine process, and also to the outer part which rests on the premaxillary. The uniting of the premaxillary with its palatine process shuts off the lower corner of the nasal cavity, which may now be regarded as the naso-palatine canal.

In fig. 4 the anterior development of the outer nasal-floor cartilage, which lies on the outer side of the naso-palatine canal, is now distinct from the anterior development of Jacobson's

cartilage, which protects Jacobson's duct on its upper, inner and under sides.

A little farther forward the two cartilages unite above, and, as shown in fig. 5, almost completely surround the naso-palatine canal and Jacobson's duct.

In fig. 6 the duct of the organ has opened into the naso-palatine canal.

On passing still farther forward, Jacobson's cartilage becomes lost, and the canal is supported above and below and on the outer side (fig. 7).

Almost at the very front of the palate, and between the two large incisors, the naso-palatine canal opens by the side of the small papilla, as shown in fig. 8.

As I have recently shown,¹ the organ of Jacobson, with its cartilages and related structures, throughout the mammalia follows one of two main types. The first is seen in its most developed, though somewhat specialised, condition in the monotremata, and in a less developed and simpler condition in the marsupialia. With slight modifications the same type is followed in the edentata and rodentia. Here the inner part of the nasal-floor cartilage becomes Jacobson's cartilage; and though the organ may either open into the posterior part of the naso-palatine canal or on to the nasal floor, the cartilage is always simple, and never has any anterior or downward prolongation away from the part forming the anterior nasal floor. In the other type, which is seen in the cheiroptera, insectivora, lemuridæ, carnivora, and ungulata, Jacobson's organ, when developed, always opens into the naso-palatine canal, and there is always a complex arrangement of the cartilages. What is manifestly Jacobson's cartilage behind, is always found, on tracing it forward, to divide into an upper part which becomes the cartilage of the nasal floor, and a lower part which passes forwards and protects the duct of the organ on its inner side. For the two groups into which the Eutheria can thus be divided, I have proposed the names—Archæorhinata and Cænorhinata.

From the examination of the organ in the Hyrax, it will be at once seen that this animal must be placed in the latter of the

¹ "A Contribution to the Comparative Anatomy of the Mammalian Organ of Jacobson," *Trans. Roy. Soc. Ed.*, vol. xxxix. pt. i., 1897, p. 231.

ns

p Pmx

- Pmx

Mx onfc

v. m. Mx

Fig. 4.

x

wx

Pmx

pc

onfc

Jc

Ja

onfc

Fig. 5.



Fig. 6.



Fig. 7.



Jc Ja n.p.c. onfc

Fig. 8.



n.p.c.

R H del

F. Huth, Lith. Edin'

ORGAN OF JACOBSON IN HYRAX.

two groups, as the relations of the organ are quite unlike those found in the rodentia and lower forms, and agree closely with those seen in the ungulata. Unfortunately the organ has only been carefully examined in a very few ungulate types; and though later researches may find in the organ of the rhinoceros or other form a closer agreement with the condition in the Hyrax, at present the organ in the Hyrax finds its nearest ally in that of the sheep and ox. The only feature of note in which the Hyrax organ differs from the normal ungulate type is in the possession of the well-developed outer nasal-floor cartilage. This is a primitive character now lost in most of the Cænorhinata, and still retained in many of the lower forms. Owing to the early obliteration of the naso-palatine canal in the horse, the condition of parts is so modified, and many of the structures so aborted, that the type is of little use for purposes of comparison. So far as can be seen, there are no features in the organ of the horse which approach more nearly to those of the Hyrax than do those of the sheep.

EXPLANATION OF PLATE XVIII..

References :—*a.n.f.c.*, anterior development of outer nasal-floor cartilage; *J.c.*, Jacobson's cartilage; *J.d.*, Jacobson's duct; *J.o.*, Jacobson's organ; *Mc.*, maxillary; *n.s.*, nasal septum; *n.f.c.*, nasal-floor cartilage; *n.p.c.*, naso-palatine canal; *o.n.f.c.*, outer nasal-floor cartilage; *Pmx.*, premaxillary; *p.Pmx.*, palatine process of premaxillary; *v.*, blood-vessels.

Fig. 1. T. section of Jacobson's organ in *Procavia*, behind anterior palatine foramen.

Fig. 2. T. section near middle of anterior palatine foramen.

Figs. 3-8. T. section through anterior palatine region, showing course of Jacobson's duct and naso-palatine canal.

IS THERE A CRITICAL PERIOD IN MARSUPIAL DEVELOPMENT? By R. BROOM, M.D., B.Sc.

FOR a good many months I have been engaged in the study of marsupial development—a work which I undertook partly to see for myself whether I could find any satisfactory evidence in support of or against the theory of vertebrate development, recently advanced by my friend Dr Beard.¹ Though, from the first, I found it impossible to believe in the occurrence of two generations between the fertilised ovum and the adult, there seemed to be brought forward in favour of there being a ‘critical period’ in vertebrates a mass of evidence sufficiently strong to compel even one who rejected the underlying theory to look into the matter. I should not at present have entered the discussion had not Dr Beard recently published² a description, with figures, of two marsupial embryos, the examination of which, he holds, proves that the marsupial is born at the ‘critical period.’ With this belief as a foundation, he has arrived at many very interesting conclusions.³ I am at present less concerned with the superstructure; but as, from an examination of the same material, I have arrived at a very different conclusion, the case is otherwise with the foundation.

Dr Beard, in his most recent publication (II., p. 87), thus defines the ‘critical period’ :—“The ‘critical period’ in a morphological sense is that epoch of the development when all the parts of the organism are first present as the foundations or ‘anlagen’ of all the organs; it is that state when epigenesis is ended, and evolution or unfolding is beginning; it is that point where the individuality of the organism is first attained, when it has ac-

¹ *On certain problems of Vertebrate Embryology*, G. Fischer, Jena, 1886.

² “The birth period of *Trichosurus vulpecula*,” *Zool. Jahrb.*, Bd. 11, 1897, p. 77.

³ *The Span of Gestation and the Cause of Birth*, G. Fischer, Jena, 1897.

These papers will in the present paper be referred to respectively by the Roman numerals I., II., and III.

quired a something setting it down as the embryo of some particular form, and—the wording is important—when it is first *beginning* to resemble its progenitors. It then bears no absolute likeness to them, but it is just *beginning* to look like them.” In other words, it is believed that when an embryo is first beginning to resemble its progenitors, all the parts of the organism are first present as the foundations or ‘anlagen’ of all the organs. The difficulty is now to decide when an embryo is beginning to resemble its progenitors; and much depends on the meaning of the word ‘resemble.’ I note that Dr Beard considers the recently born *Macropus thetidis* (?)¹ to be “quite like a kangaroo” (II., p. 91). If this is an illustration of the meaning to be attached to the words “quite like,” the difficulty of picturing an embryo that is “beginning to resemble” its progenitors is enhanced. We are, however, assisted by the furnishing of a number of guides, by which, from the external characters, the ‘critical period’ can be determined (II., p. 88). These are:—“the mammary line has just entirely disappeared, and has left a certain number of well-defined milk points, the lacrymal groove has quite disappeared, hair follicles are visible on some part of the face, the eyes are ovoid and no longer rounded (Keibel), the forearm is flexed, and the digits of the hand are easily made out.” While admitting that “sometimes all these tests cannot be applied, as in the sheep, where a mammary line is never developed,” Dr Beard adds that, “practically, hardly one of them can be applied to marsupial embryos.” At birth, and for a considerable time afterwards, marsupial embryos are furnished with a thick epitrichial layer, which no doubt hides the external characters to some extent, but this layer is only formed as the embryo is approaching birth, and in all the earlier stages the external characters are as distinct as in a Eutherian foetus.

If, furnished with these guides, a series of marsupial embryos be examined, in an endeavour to find a ‘critical period’ such as has been described in the Eutheria, there would be little diffi-

¹ The species of this foetus, which I gave to Dr Beard, must be regarded as doubtful. It was given me as the young of a ‘Paddymelon’; but as this form was very rare in the district, and the intelligence of the man who collected it for me was not above the average, I was careful to query the species. I pointed out the uncertainty to Dr Beard, but, from his paper, he evidently considers no doubt exists.

culty in deciding on one much before birth as coming nearest to the looked-for stage. Take, for example, an intrauterine *Trichosurus* embryo of 10·5 mm., greatest length. Here there is no obscuring of the external characters by a thick epitrichial layer, and we find the head bearing a greater resemblance to the progenitor than even at birth. The lacrymal grooves are closed, and the face is better formed than in the human embryo of over 7 weeks. The eyelids are open, and give the small eye an oval appearance; the external ear is quite distinct, and the pinna pointed. The fore-limbs are well formed; and the digits are not only distinct, but are already provided with claws. The hind-limbs are, of course, less developed; but even here the digits, though still attached to each other, are clearly mapped out. When the internal anatomy is examined, the chorda dorsalis is found to be constricted by well-developed cartilaginous vertebral centra, which are cartilaginous even to the root of the tail. The ribs, fore-limbs, and shoulder-girdle are also well chondrified, and the clavicle is ossified. Jacobson's organ is developed, and the retina pigmented partly. The development of the permanent kidneys and of the Muellerian ducts has advanced some little distance; while the dental ridge is laid down, and the incisor germs well developed. With the exception of the non-differentiation of sex, which is a character apparently of slight moment in the determination of the 'critical period,' since it is admittedly absent in the majority of the Ichthyopsida (I., p. 11), in two points only is the 10·5 mm. *Trichosurus* behind the embryos of the mole, rabbit, and pig described as 'critical':—(1) there is no commencement of the posterior fissure of the spinal chord, and (2) there is a lumen in the lens. As Dr Beard admits that there is still a cavity in the lens at the birth period, it must be assumed that he does not regard the obliteration of the cavity in the lens as a necessary character of the 'critical period.' We are thus left with only one essential feature in which the 10·5 mm. *Trichosurus* is behind the supposed critical Eutherians, while, as regards its skeletal development, it is far in advance.

Let us now consider the stage in the development which Dr Beard considers to represent the 'critical period.' As all the adult internal organs are either originated or considerably developed in the 10·5 mm. *Trichosurus*, of course they are equally

to be found in all the later stages. But if we are to wait till the birth period to get a stage corresponding to the 'critical period' of the pig, rabbit, or mole, we shall find, on careful examination, that we are much farther off than before, on the other side. The brief period during which Dr Beard had to examine the sections of the late intrauterine and just-born *Trichosurus* might readily excuse the omission to observe certain points; but, unfortunately, in the points described, Dr Beard has made one or two rather serious mistakes in observation. He says—(II., p. 86):—"Whereas in no other cases known to me is the skeleton, at the 'critical period,' other than cartilaginous in the marsupial, as exemplified by *Trichosurus*, there is, at this epoch, bone in the form of a largely ossified clavicle." This observation as regards the clavicle is correct, as I pointed out about a year ago,¹ but it implies, unfortunately, that the clavicle alone is ossified; and on page 82 (II.) the definite statement is made, while giving the characters of the newly-born specimen, that "there is, as yet, no ossification in the lower jaw." That Dr Beard evidently considers the presence or absence of ossification in the lower jaw a point of much importance in the determination of the 'critical period' may be seen from the following statement on page 90 (II.):—"The newly-born *Perameles obesula* is over the 'critical period,' and this is proved by, among other things, the circumstance that ossification has then set in [in] the lower jaw." The true facts with regard to the newly-born *Trichosurus* are, that not only is there an extensively ossified lower jaw, but that many other bones of the head are also well ossified. Ossification is well marked in the following bones:—premaxillary, maxillary (with even the secondary palatal plate formed), palatine, and pterygoid. In the late uterine fetus the same bones are all ossified, with the exception of the pterygoid. Fig. 1 represents a cross-section of the snout of the unborn specimen, and shows the degree of ossification of the jaws.

Notwithstanding the assertion on page 87 (II.) that "what really determines the critical period . . . is the state of the embryo as a whole, and not the histological condition of some one or more organs of secondary importance," Dr Beard seems to

¹ "On the Existence of a Sterno-coracoidal Articulation in a Fœtal Marsupial," *Jour. Anat. and Phys.*, July 1897.

take the single character of the commencement of the posterior fissure of the spinal cord as his guide in determining the 'critical period'; and if his tables of the 'critical period' be examined, it will be found that, with the exception of such characters as "adult form of olfactory organ," which would equally suit any of the later stages, it is the only character which the various embryos described as 'critical' have in common.

In marsupials, so far as my researches go, the posterior fissure is always formed at a very late period in the development, as compared with that in the Eutheria. In *Trichosurus*, Dr

FIG. 1.—T. S. of snout of late intrauterine fetus of *Trichosurus*. $\times 20$.
Showing degree of ossification of the jaws.

Beard states that the posterior fissure is "well initiated" at birth, and this he evidently considers a very strong point in support of his belief that the 'critical period' occurs at exactly the same time. Being unable myself to find any indications of a posterior fissure at birth, and thinking it probable that Dr Beard, with his much larger experience, might possibly have seen some evidences that had escaped me, I cut an embryo *Trichosurus* of 17 mm. (greatest length), and here I found on examination that the posterior fissure is no more initiated than at birth. As I will shortly elsewhere be illustrating the development of the spinal cord in *Trichosurus*, I will at present give a figure of the condi-

tion in a mammary foetus of the ring-tailed phalanger, *Pseudochirus peregrinus*. Figure 2 represents a section of the spinal cord of a 16 mm. mammary foetus of this interesting form, which, by the way, is considerably smaller at birth than *Trichosurus*. To illustrate the degree of development of this foetus, it may be mentioned that, besides having a highly ossified condition of many of the bones of the head, ossification had commenced in the arches of the cervical vertebræ, the upper ribs, the long bones of the fore-limbs, and the scapula, and, of course, in the clavicle. A

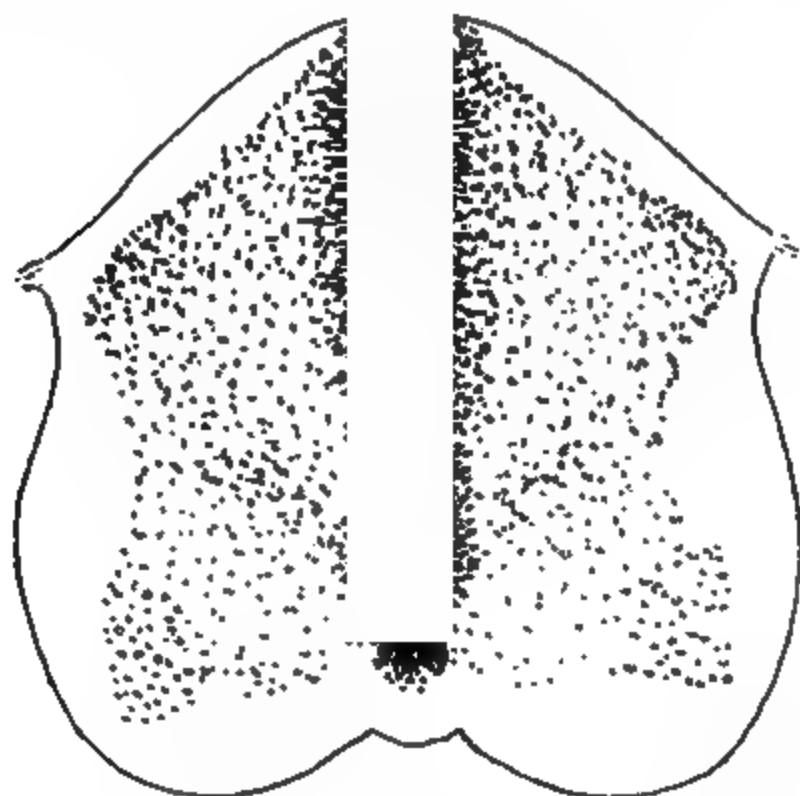


FIG. 2.—T. S. of spinal cord of 16 mm. mammary foetus of *Pseudochirus peregrinus*, in the cervical region. $\times 90$.

glance at the figure will readily suggest how "well initiated" the posterior fissure must be at birth in this form, and will show how reliable is "the best and surest guide" (III., p. 103) among the internal characters to the supposed 'critical period.'

It will thus be seen that, so far from there being any evidence to be derived from a study of marsupials in favour of there being a 'critical period' in mammalian development, there is very strong reason for regarding the 'critical period' as purely imaginary, and that some of its main foundations rest on inaccurate observations.

To one who fails to see anything 'critical' in the condition of the marsupial at birth, the most interesting feature is that it is in many of its characters a monotreme. It has a cloaca; and, as I have already shown, the coracoid is well developed, and articulates with the sternum; while the ear, which Dr Beard notes to be of the "mammalian type," differs from that of the adult marsupial and Eutherian, and agrees with that of the monotreme in having the cochlea not spiral, but only slightly curved.

THE MUSCLES OF MAMMALS, WITH SPECIAL RELATION TO HUMAN MYOLOGY: A COURSE OF LECTURES DELIVERED AT THE ROYAL COLLEGE OF SURGEONS OF ENGLAND, by F. G. PARSONS, F.R.C.S., *Hunterian Professor*.

(Continued from page 450.)

LECTURE II.—THE MUSCLES OF THE SHOULDER AND FORE-LIMB.

Deltoid.—In man there are three parts of the deltoid recognised—clavicular, acromial, and spinous; these are so closely connected that any attempt to separate them would result in an artificial division. In apes and monkeys the three parts, although more easily separable, are still united, while in lemurs the spinous part of the muscle is separate, and inserted deep to, and nearer the shoulder than, the acromial portion (fig. 1). In most clavicate animals lower down in the scale, such as the bats, rodents, and insectivores, the three parts are quite distinct, and the clavicular fibres are attached lower down (nearest the elbow), the acromial fibres deep to these and nearer the shoulder, while the spinous fibres are inserted highest of all, and deep to the acromial ones. In the non-clavicate animals, such as carnivores and ungulates, the clavicular portion of the deltoid is continuous with the cephalic fibres of the trapezius, to form the cephalo-humeralis. This muscle has a tendinous intersection marking the line of the absent clavicle, and here the cleidomastoid muscle is also attached. In most carnivores a rudimentary clavicle is present, though this does not take the place of the tendinous intersection, but lies deep to it. Very often the clavicular head of the deltoid is inserted into the forearm with the biceps and brachialis anticus; this is especially the case in animals belonging to the families of Felidæ and Viverridæ among the Carnivora.

The overlapping of the three parts of the deltoid reminds us of a similar arrangement in the pectorals: here the clavicular

part is most superficial and inserted lowest, the sternal fibres deeper and nearer the shoulder, while the abdominal fibres or

FIG. 1.—Shoulder muscles of Lemur. *a*, omo trachelian; *b*, cleido-mastoid; *c*, sterno-mastoid; *d*, trapezius; *e, e', e''*, three parts of deltoid; *g*, *teres major*; *h*, *triceps*; *j*, *latissimus dorsi*.

pectoralis quartus are inserted deepest and highest of all. A similar arrangement of fibres may be noticed in the *subscapularis* of some mammals, *e.g.*, the dog: here the fibres which rise highest

pass superficial to the others, and are inserted lowest (fig. 2). What the original cause of this twisting of the muscles about the shoulders is I do not know, though it is easy to see a mechanical advantage in it. The facts, however, are worth bearing in mind by future observers.

Teres minor.—The teres minor is usually regarded as a separate slip of the deltoid; and when we look at the arrangement of the spinous head of that muscle in a generalised mammal, such as

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FIG. 2.—Arm muscles of Dog (*Canis familiaris*), showing the arrangement of the Subscapularis and the Coraco-brachialis brevis. (From the *Proceedings of the Zoological Society*).

the dog, it is easy to imagine how some of the anterior (cephalic) fibres might have acquired an attachment to the axillary border of the scapula and to the fascia over the infraspinatus; they would then run from the axillary border of the scapula to the humerus just below the shoulder joint. Higher up in the mammalian scale, the spinous head of the deltoid shifts its insertion to nearer the elbow, but the teres minor bundle retains its original insertion. This shifting downwards of the attachment of the spinous part of the deltoid must, I think, be dependent on the conversion of the fore-limb in the primates from

an organ of locomotion to one of prehension, though it is difficult to define the exact mechanical advantage of the change, as we know so little of the combinations of muscles which produce any definite movement. It may be objected that the lemurs are distinctly brachiating animals, and that in them the spinous

FIG. 3.—Arm of *Macacus rhesus*. *a*, Deltoid (cut); *b*, Supraspinatus; *c*, Infraspinatus; *d*, Teres minor; *e*, Muscular slip; *f*, Brachialis anticus.

portion of the deltoid has its typical mammalian insertion near the shoulder. To this I would reply, that muscles often take a long time to adapt themselves to the altered habits of their possessors: for example, the muscles of the arboreal squirrel hardly differ at all from those of the burrowing marmot; and it

may well be that, in the lemurs, the adaptation of the deltoid to altered habits, an adaptation so evident in monkeys and man, has not yet had time to be acquired.

In one macaque monkey which I dissected, and of which I show a specimen (fig. 3), a muscular slip passed from the metacromion where the deltoid was rising, to the axillary border of the scapula at the origin of the teres minor. I have never seen or heard of this muscle before, but I have in three or four cases, *e.g.*, *Rhizomys*, *Myopotamus*, and *Pedetes*, found a fibrous band occupying exactly the same position, and having the same

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FIG. 4.—Shoulder muscles of Bamboo Rat (*Rhizomys badius*). (From the *Proceedings of the Zoological Society*.)

direction and relations (fig. 4). I look upon this muscle as an evidence of the original connection between the deltoid and teres minor. Of course, the strongest reason for regarding the teres minor as part of the deltoid is the common nerve supply from the circumflex.

Coraco-brachialis.—This muscle was described by Wood as consisting of three parts, the coraco-brachialis brevis or rotator humeri, which is only present as an abnormality in man, and which is always inserted above the tendon of the latissimus dorsi (fig. 2); the coraco-brachialis medius inserted into the middle of the shaft of the humerus; and the coraco-brachialis longus

inserted into the internal condyle or just above it. Testut, I think very wisely, separates the brevis from the rest, and describes it as a distinct muscle: I propose to follow his example. The coraco-brachialis brevis is found in the Monotremes, Ornithorhynchus, and Echidna; in Didelphys, Thylacinus, Sarcophilus, Dasyurus, Cuscus, and the Macropodidæ (in spite of Meckel) among the Marsupialia. In Tatusia, Orycteropus, and Chlamydophorus among the edentates, but not in Myrmecophaga, Tamandua, or Cyclothurus. In Balænoptera, Phocæna, and Globiocephalus among the Cetacea, but not in Hyperoodon. In Sus, Bos, Ovis, and Equus among the ungulates, but not in Hippopotamus or Procavia (Hyrax). In the rodents the coraco-brachialis brevis is present in all the sciuromorphic and lagomorphic forms, while in the hystricomorphic and myomorphic it is only occasionally found. The Carnivora are remarkable for always possessing this muscle except in certain members of the Mustelidæ or weasel family; for instance, it was absent in five otters, three polecats, and a badger, of which I have records. Among the insectivores it is present in Galeopithecus, Erinaceus, Centetes, Solenodon, and Potamogale, but is absent in Gymnura and the Talpidæ. In the Cheiroptera it is always absent. Among the Primates it is present in lemurs, and in cynomorphous monkeys, according to Keith, it is rarely absent. In chimpanzees (Anthropopithecus) it is present in over 30 per cent., but in gorillas and oranges it is less frequent. In man, according to Wood, it is found in about 3 per cent. of all cases. The facts which stand out most clearly from this resumé are:—(1) that the muscle tends gradually to disappear in the primates until man is reached, when its disappearance is almost complete; (2) that the muscle is absent in bats; (3) that in all the other orders it is usually present, but occasionally absent. We have seen that the omo-hyoid and omo-trachelian muscles of man and bats differ from those of other mammals, and we have traced this resemblance to the setting back of the shoulders. I cannot help thinking, though I do not know how it happens, that the absence of the coraco-brachialis brevis may be due to, or correlated with, the same cause.

The coraco-brachialis medius and longus are muscles which are not very satisfactorily separated from one another. The medius

arises from the coracoid process, and is inserted into near the middle of the shaft of the humerus, passing ventral to the tendon of the latissimus dorsi (fig. 5, *a*). In man this part of the muscle is pierced by the musculo-cutaneous nerve, but in every other mammal which I have dissected I have always found the nerve passing above the medius. There are, however, records of oranges and chimpanzees in which the nerve has been found piercing the

FIG. 5.—Arm of Tree Porcupine (*Sphingurus prehensilis*). *a*, coraco-brachialis medius; *b*, coraco-brachialis longus; *c*, biceps; *d*, median nerve; *e*, musculo-cutaneous nerve; *f*, epitrochleo-aneconeus; *g*, brachialis anticus; *h*, pectoral; *i*, deltoid; *k*, claviculo-scapularis; *l*, latissimus dorsi; *m*, dorso-olecranal.

muscle, and there are also some of gorillas in which there is a continuity between the coraco-brachialis brevis and medius. I do not think that man's coraco-brachialis represents the fused upper and middle heads of other mammals, because an upper head is, as we have seen, sometimes present in man, with its normal insertion above the latissimus dorsi: moreover, the relation of a nerve to a muscle is not a point on which too much stress should be laid; every anatomist is familiar, for instance, with

the way in which the great sciatic nerve sometimes pierces the pyriformis, and at other times passes deep to it. My own opinion is that the coraco-brachialis of man represents the medius of the lower animals, and that possibly the longus may be represented by the internal intermuscular septum.

The coraco-brachialis longus arises from the coracoid process, and is inserted into the lower end of the humerus above the internal condyle; in many cases it is difficult to determine where the separation between it and the medius occurs, but sometimes in man the two parts are separated by the median nerve and brachial artery. I have only once found this arrangement in the lower mammals, in a tree porcupine (*Sphingurus*), and I have never met with any record of it by other writers (fig. 5). The animals in which the longus is best developed are not confined to any special order; it is found in *Cuscus* among the marsupials, in *Tatusia* and *Orycteropus* among the edentates, in *Erinaceus*, *Centetes*, and *Solenodon* among the insectivores. In the rodents it is present in the tree porcupines *Erethizon* and *Sphingurus*; in many squirrels (*Sciurus*, *Pteromys*, *Xerus*, and *Spermophilus*), as well as in most of the *Myomorpha*. It is present in the bears among the *Carnivora*, in the ox and sheep among the *Ungulates*, and in many lemurs. It is a curious fact that in three animals no trace of any part of the coraco-brachialis has been seen: these are the African polecat (*Ictonyx*) among the *Carnivora*, *Gymnura* among the *Insectivora*, and *Viscacha* among the *Rodentia*. My own experience of each of these animals is confirmed by that of other observers. As far as I know, these animals have nothing in common, either in their structure or habits, which can account for the total disappearance of the muscle.

Brachialis anticus (Flexor brachii brevis).—In man this muscle is very imperfectly developed. If we examine any mammal in which the muscular system is fairly generalised, such as a rodent or insectivore, we shall find that the greater part of the muscle rises from the back part of what in man is the surgical neck of the humerus, and that the fibres wind round the outer side of the bone, to be attached to the ulna just below the elbow. In addition to this, we can often separate an internal slip (*e.g.*, in *Hystrix* or *Dasyprocta*) which arises from

the front of the humerus below the pectoral ridge, and just internal to the insertion of the coraco-brachialis medius (fig. 5). In a three-toed sloth (*Bradypus*) which I lately dissected, the coraco-brachialis was almost continuous with this part of the brachialis anticus, and the direction of the fibres was the same.

I look upon the external part of this muscle as a combination of the fibres of the dorsal and ventral part of the sleeve-like process which is pushed out from the trunk musculature by the budding anterior extremities: this view accounts for its dorsal origin and ventral insertion, as well as for its double nerve supply by the musculo-spiral, which is a dorsal branch of the brachial plexus, and the musculo-cutaneous, which is a ventral nerve. The supinator longus and extensores carpi radiales were probably the original downward continuation of this sheet, but they have acquired a secondary attachment to the outer (pre-axial) condyle of the humerus, and only the fibres which were ventral to them are continued on as the insertion of the brachialis anticus. With one or two exceptions (*Bradypus*, *Pteropus*, etc.), the high origin of the muscle persists until we reach the anthropomorphine apes; then the upper part of the outer head dwindles, and only remains as a few fibres rising from the floor of the spiral groove, a groove which was evidently formed primarily by the brachialis anticus, not by the musculo-spiral nerve, for which it is much too large.

The fact that in man the origin of the brachialis anticus dovetails to receive the insertion of the deltoid is explained by regarding this as the point of union between the original external and internal heads of the double muscle. With regard to the nerve supply, I have frequently observed that in mammals the outer (long) head is supplied by both the musculo-cutaneous and musculo-spiral nerves, while the inner head only receives twigs from the musculo-cutaneous. Macalister notices that the human brachialis anticus receives an external and internal branch from the musculo-cutaneous, another indication of the original double nature of the muscle.

Palmaris longus.—This muscle is almost as inconstant in the lower mammals as it is in man. Sometimes it is a distinct muscle, at others it is a slip from the inner part of the surface of the flexor sublimis digitorum, as in the paca (*Cœlo-*

genys) and ground squirrel (*Xerus*), while at others it comes from the surface of the flexor carpi ulnaris, *e.g.*, civet (*Viverra*), both these latter arrangements are known as abnormalities in man. In a kinkajou (*Cercoleptes*) and a genet (fig. 6) the two varieties coexisted in the same forearm, and it was noticed that the one derived from the flexor carpi ulnaris was supplied by the ulnar nerve. I am quite in accord with the theory that the palmaris longus is a degenerate flexor of the proximal phalanges.

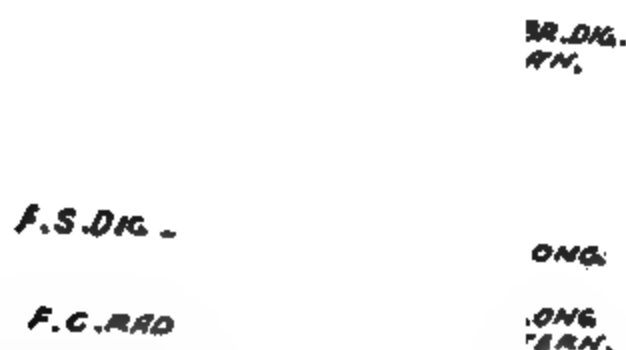


FIG. 6.—Forearm of Genet (*Geneta vulgaris*), showing two *Palmares Longi* and *Flexor Brevis Digitorum Manus*. (From the *Proceedings of the Zoological Society*.)

and it is possible that the muscle was originally a broad sheet, supplied by both median and ulnar nerves.

Flexor sublimis digitorum.—All through the mammalian class this muscle seems to be going through a continual struggle to maintain its existence, or, at least, to avoid becoming a mere muscle of the carpus, as it is in the hind-limb a muscle of the tarsus. In spite of the fact that many reptiles have a flexor perforatus rising from the carpus, it seems probable that the origin from the internal condyle is the more primitive. The commonest insertion of the muscle is into the middle phalanges of the four ulnar digits; occasionally there is a tendon for the

pollex also, though it does not seem to be constant for any animal or group of animals. After that to the pollex, the minimus tendon is the one most frequently wanting, but on several occasions when this has happened I have found, on slitting up the theca, the perforated loop of the tendon surrounding the flexor perforans, and having its usual insertion, although there was no tendon, in the hand and forearm to this digit. This arrangement I found in the paca (*Cœlogenys*), rock

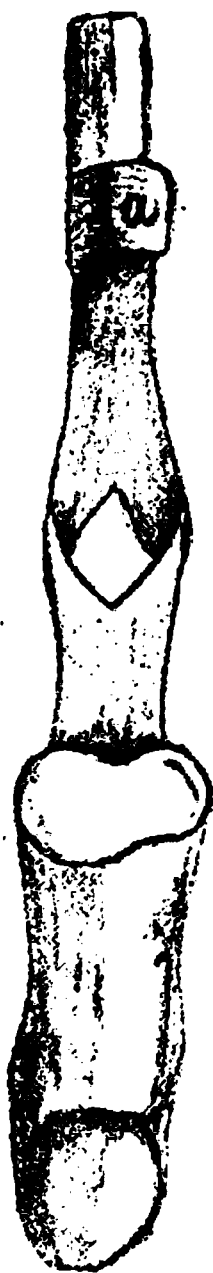


FIG. 7.—Human Flexor Sublimis Digitorum. (From a specimen in the R.C.S. Museum). *a*, Ring surrounding flexor profundus tendon.

kangaroo (*Petrogale*), and other animals. Sometimes the muscle only sends tendons to two digits; this was noticed in the bear, otter, badger, etc., but each case seems to have been an exceptional one. In the rodents, carnivores, and insectivores, a ring passes from the sublimis tendon just before it is perforated, and this surrounds the profundus tendon, which then perforates the sublimis, as in man. There is a specimen of a human flexor sublimis tendon in the museum of this College, which shows an

identical ring in the same position; it is, however, only feebly developed. I do not know whether this is an occasional atavistic structure in man, or whether it is always present, and only requires careful looking for.

In the three-toed sloth (*Bradypus*) the flexor sublimis is absent altogether. Sometimes the work of this muscle is partly undertaken by one which rises from the pisiform bone or anterior annular ligament, and which is called by Mivart and Murie the flexor brevis digitorum manûs (figs. 6 and 8); it is best seen in *Procavia* (Hyrax), where the above-named investigators found it.

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FIG. 8.—Manus of *Ichneumon* (*Herpestes griseus*). (From the *Proceedings of the Zoological Society*.)

passing to three digits; I have often found the muscle in rodents and carnivores, but have never seen it going to more than the two ulnar digits. As a rule, the tendon of the flexor brevis takes the place of that of the flexor sublimis to a digit, but this is not always the case, for in some of the hystricomorphine rodents the two tendons coexist, and join one another in the theca of the digit. On the whole, it seems to me probable that the flexor brevis digitorum manûs represents some of the ulnar fibres of the flexor sublimis which have acquired an attachment to the pisiform bone or annular ligament, and of

which the forearm portion has been suppressed. The resemblance of this muscle to the flexor brevis digitorum pedis will be evident to everyone. The accessory heads of the human flexor sublimis are only found in monkeys. In the cynomorpha, two heads often come from the internal condyle; it is probable that as the individual use of the digits becomes more important, the lower one of these enlarges and spreads down the internal

FIG. 9.—Flexor Profundus of Hedgehog (*Erinaceus Europæus*). *a*, condylo-radialis; *b*, condylo-ulnaris; *c*, condylo-centralis; *d*, ulnaris; *e*, radialis.

lateral ligament of the elbow to the inner side of the coronoid process. The radial head from the oblique line is only found in the anthropomorpha.

Flexor profundus digitorum.—Windle has given by far the most satisfactory account of the morphology of this muscle that I know. He says that typically it is made up of five portions, which join a little above the wrist. These are named—(1) radio-condylar; (2) ulno-condylar; (3) centro-condylar; (4) radial;

(5) ulnar. Of these, the radial and ulnar are the most constant, and the centro-condylar least frequently seen; but almost any combination may occur. There is an insectivorous animal named *Gymnura*, which this College has recently given me the opportunity of dissecting, and in which, from the very generalised condition of its muscles, I expected to find all five parts of the flexor profundus. In this I was not disappointed, and I have since found that its near relation, the hedgehog (*Erinaceus*), has the same arrangement (fig. 9). When the different parts of the muscle have united, which occurs in the lower part of the forearm, Keith has shown that each digit typically receives fibres from the radial and ulnar portions, though in many cases one or other of these may be suppressed. In man the radial portion of the muscle goes entirely to the pollex, and the radio-condylar is often present as an extra origin of the flexor longus pollicis, which has slipped down from the condyle to the inner side of the coronoid process. Macalister looks upon it as the remains of an obsolete superficial flexor of the thumb, but I find it hard to agree with him, because I have records of a cat, two bears, a racoon, and a coati, in which the flexor sublimis sent a slip to the thumb, and in which the radio-condylar head of the flexor profundus was also present. The ulno-condylar head is occasionally seen in man, and rises from the condyle or the deep surface of the flexor sublimis. During the winter session of 1896-97, there was in the dissecting-room of St Thomas's Hospital a condylo-ulnaris and condylo-centralis in the same forearm, the latter being attached, as is usual in mammals, to the flexor profundus close to the wrist.

Flexor carpi ulnaris.—This is a very constant muscle in mammals. The chief point of interest that I have noticed about it is its tendency in certain of the carnivora, notably the family of the Canidæ, to form two distinct muscles, condylo-pisiform and olecrano-pisiform, both of which are supplied by the ulnar nerve. In the human muscle I have, on several occasions, noticed that two twigs are given off by the ulnar nerve to the flexor carpi ulnaris, and that these are distributed to the condylar and olecranal heads of the muscle respectively. This arrangement, if it be at all constant, I should regard as a relic of the former division of the muscle into two parts.

Pronator radii teres.—The superficial head is the only part of this muscle which is present in mammals until the anthropoid apes are reached. Keith records the deep or coronoid head as being present in all the recorded cases of oranges, in 90 per cent. of chimpanzees, and in 40 per cent. of gorillas. Macalister points out that this deep head is probably derived from some of the fibres of the pronator quadratus, which often extends for the whole length of the radius and ulna. The insertion is variable, but seldom extends above the middle of the radius, though in many animals, *e.g.*, bears, porcupines, etc., it reaches the lower end of the bone. In ungulates the muscle is extremely rudimentary, and is absent altogether in the horse. Lesbres has recently pointed out, however, that it occasionally occurs as a vestigial structure in that animal.

Supinator longus.—This muscle, as has been mentioned, is probably a continuation downward of the brachialis anticus sheet, and the two muscles are always separated with some difficulty. One of the commonest variations in man is to find a more extensive origin from the humerus than usual. Testut mentions the otter, the cat, the two-toed sloth, and the wombat as animals in which the muscle rises from a very large extent of the humerus. I can confirm his statement with regard to the otter and cat; indeed it is true for most of the Felidæ. The insertion is sometimes in man continued on to the carpus: this I have found to be a characteristic of the jerboa family (Dipodidæ), besides occurring in some kangaroos, though not in all. Young has also noticed it in the koala (*Phascolarctus*). In the fruit bat (*Pteropus*) I have found it inserted into the fascia of the forearm, at the junction of the upper and middle thirds, and this agrees with the dissections of Humphry and of Macalister. The muscle is described as being sometimes double in man, but I have never been fortunate enough to see it either in him or in any lower mammal. In the cynomorphous monkeys the muscle is, as a rule, better developed than in man, and Keith mentions that it is often continued on to the external lateral ligament of the wrist: this he regards as possibly an indication that the muscle was originally a flexor of the pollicial metacarpus. The supinator longus is sometimes absent in man; it is also absent with great constancy in many groups of mammals. This is the case in all

the insectivora, in the Canidæ, and Hyænidæ, among the Carnivora, and in many families of the Rodentia.

Supinator brevis.—In all mammals below the Primates the supinator brevis consists of only one layer which lies entirely superficial to the posterior interosseous nerve; in the lemurs, however, we begin to find another layer developed deep to the nerve, and this arrangement persists throughout the monkeys, apes, and man. In dissecting the forearm of a racoon (*Procyon lotor*) I was struck by the fact that the highest fibres of the extensor ossis metacarpi pollicis were slightly overlapped by the supinator brevis, and extended up to just below the lesser sigmoid cavity of the ulna. It occurred to me that the deep layer of the supinator brevis was possibly derived from an extension upward of the extensor ossis metacarpi pollicis plane of fibres, which, instead of being continued down to the thumb, had acquired a secondary attachment to the radius. In the lower mammals the supinator brevis is a vertical narrow bundle; but as one ascends in the scale of the primates, both layers become more and more broadened out, and the direction of their fibres more oblique. Of course, in the case of the supinator brevis, as in that of the pronator radii teres, the conclusion which we came to with regard to the coraco-brachialis must be borne in mind: it was there suggested that the musculo-cutaneous nerve had, so to speak, sunk into the middle part of the muscle, and it is possible that in the same way the median nerve might have passed through the originally single pronator radii teres, or the posterior interosseous through the supinator brevis. The supinator brevis, however, differs from the coraco-brachialis or pyriformis of man in that we can see some transitional stages in the appearance of the deep layer: in the lemur, for instance, it is very small, and quite distinct from the superficial one, rising from the orbicular ligament, and being inserted into the neck of the radius, while in the monkeys and apes it is larger, and becomes more and more closely united with the superficial layer.

LECTURE III.—MUSCLES OF THE HIND-LIMB.

Ectogluteus.—The ectogluteus or gluteus maximus of man is a muscle specialised for adapting the body to the erect position. In most other animals its iliac origin is wanting, and it is found as a thin muscular plane, rising from the spinous process of the sacral and anterior caudal vertebræ. Its anterior fibres are inserted into fascia, and are often inseparable from those of the tensor fasciæ femoris, though sometimes there may be a con-

FIG. 10.—Outer side of thigh of Guinea pig (*Cavia cobaya*). *a*, ectogluteus; *b*, tensor fasciæ femoris; *c*, sartorius; *d*, caudo-femoralis (*Agitator caudæ*); *e*, flexor cruris lateralis (biceps); *f*, semitendinosus.

siderable interval between these two muscles, in which the mesogluteus comes to the surface. The posterior fibres are attached to more or less of the shaft of the femur, and are continuous with those of the agitator caudæ (caudo-femoralis) when that muscle is present (fig. 11); when it is absent, the borders of the ectogluteus and flexor cruris lateralis (biceps) are in contact. *Gymnura*, which serves as an extremely good type for studying mammalian myology, shows that the sartorius (ilio-tibialis), the tensor fasciæ femoris, the ectogluteus, and the biceps (flexor cruris lateralis) are all in one plane, and near their origins are

inseparable: it further shows that this superficial sheet is supplied by branches from the anterior crural ventrally, then by twigs emerging from the great sciatic notch ventral to the pyriformis (superior gluteal nerve of man), then by twigs emerging dorsal to the pyriformis (inferior gluteal and nerve to the hamstrings). The ilio-tibialis or sartorial part of this sheet in *Gymnura* is well developed and reaches the tibia, but in most

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FIG. 11.—Thigh of Dog (*Canis familiaris*) from outer side. (From the *Proceedings of the Zoological Society*.)

rodents and many carnivores and marsupials it ends in the fascia on the extensor surface of the thigh. In the closely allied families of the Canidæ and Hyænidæ among the carnivora the muscle is always double, the anterior part going to the patella, the posterior to the tibia. The most posterior fibres of the ectogluteus, those coming from the anterior two or three caudal vertebræ, often form a distinct muscle, the agitator caudæ.

Windle and I have suggested caudo-femoralis as a better name, since it does not commit us to views on the action of the muscle. The development of the muscle does not depend on the size of the tail: it is well developed in the guinea-pig, for instance (fig. 10), and absent in the dog (fig. 11). In the Felidæ it is usually attached by tendon to the side of the patella, but in most mammals in which it is present it is inserted into the lower part of the femur. It will be seen that this muscle forms a connecting link between the ectogluteus and the flexor cruris lateralis (biceps), and it is not surprising that, where it is not specially looked for, it is often described as part of one of these.

Flexor cruris lateralis (Biceps).—This muscle has a very constant origin from the tuber ischii, and is often reinforced by a more superficial head from the transverse processes of some of the anterior caudal vertebræ. The usual insertion is into the fascia on the outer side of the upper two-thirds or so of the leg (fig. 10). The animal in which I have seen it most fully developed is *Gymnura*: here it is inserted into the lower part of the shaft of the femur, into the outer side of the patella, and into the fascia of the outer side of the whole length of the leg. In many rodents the caudal and ischial parts are quite separate; and when this is the case, the caudal portion is inserted into the patella and the ischial into the fascia of the leg: it is probable that the caudal portion here represents an agitator caudæ.

In many carnivores, insectivores, and kangaroos the lowest fibres have been found to make a sort of sheath for the tendo Achillis, and to be inserted into the calcaneum and plantaris tendon; how far this is the case in other animals I do not know. In the primates the caudal head disappears, but in young animals part of the origin can be traced into the great sciatic ligament: this is probably a remnant of the caudal head. The fascial insertion in the lower leg is well marked in the lemurs and cynomorphous monkeys, but in the anthropoids it is chiefly confined to the upper part of the leg, and attachments to the outer tuberosity of the tibia and head of the fibula become more important. The short or femoral head, foreshadowed in certain edentates (pangolin, three-toed sloth, etc.), is found in the New World howling and spider monkeys, as well as in the anthropoids. I have lately looked for this short head carefully in two

animals in which I expected to find it: one was the great anteater (*Myrmecophaga jubata*), and the other a spider monkey (*Ateles*). As far as I know, there is no detailed description of the muscles of the hind-limb of the former animal, and I therefore feel justified in detaining you for a minute or two to consider the arrangement of its biceps (fig. 12). The long or pelvic head arises as usual from the tuberosity of the ischium, and is inserted by a fascial tendon into the upper part of the outer side

FIG. 12.—Outer side of thigh of Great Anteater (*Myrmecophaga jubata*).
a, ectogluteus; *b*, vastus externus; *c*, caudo-femoralis; *d*, long head of flexor cruris lateralis (biceps); *e*, short head of flexor cruris lateralis (biceps); *f*, semitendinosus; *g*, gastrocnemius.

of the leg, but there is no insertion into the patella, as is so often the case in mammals. The short or femoral head rises from the surface of the caudo-femoralis or agitator caudæ, and, instead of joining the long head, passes deep to it, and is inserted into the gastrocnemius about the middle of the leg. The two muscles thus form an X. In *Ateles* it is interesting to find that the arrangement is almost identical: the short head rises from the femur below the middle, and is inserted into the upper part of

the shaft of the fibula, passing deep to the long head, and forming the same X-like figure.

Tenuissimus.—In a generalised mammal such as a carnivore or insectivore, a long riband-like muscle is found rising from the anterior caudal vertebræ, and passing deep to the flexor cruris lateralis, but superficial to the great sciatic nerve. In the lower part of the leg it joins the lowest and most posterior fibres of the last-named muscle, to assist it in forming a sheath for the tendo-Achillis. It is sometimes called the 'bicipiti accessorius,' and is of interest because it may be represented in man by a slip which occasionally passes from the biceps to the gastrocnemius or tendo-Achillis. The muscle is best seen in the carnivora and insectivora, though even in these it may be partially fused or suppressed. In the ungulata and primates it is not normally present.

Semimembranosus and Pre-semimembranosus (Ischio-supra-condyloideus).—It has long been understood by anatomists that the portion of the human adductor magnus, which rises from the tuber ischii, and which is inserted into the adductor tubercle above the internal condyle of the femur, is really a portion of the semimembranosus, which carries its original nerve supply to its new locality. After examining a good many animals, I believe that the most generalised arrangement is that which is met with in most insectivores and carnivores: here the semimembranosus and pre-semimembranosus form a single muscle at their origin from the tuber ischii, and divide above the middle of the thigh, so that in these animals it would be more convenient to speak of the mass as a single muscle with a double insertion. In some insectivores, many rodents, and most monkeys, the pre-semimembranosus is distinct from the semimembranosus in its whole extent; while in the rat, the porcupine, and a few other rodents, it has a perfectly separate origin from the anterior caudal vertebræ. In three specimens of lemurs which I have examined (fig. 14), I have remarked the complete absence of all trace of the pre-semimembranosus, and I can find no mention of the muscle in Mivart and Murie's work on the lemuroidea. I feel sure that, had it been present in their specimens, they would have figured and recorded it, and I think there is every reason to believe that the absence

of a pre-semimembranosus is a characteristic of lemurs. In kangaroos and most sciuromorphic rodents the muscle, instead of being separate, is closely blended with the adductors as in man. It is interesting to note that, according to Keith, the pre-semimembranosus remains a separate muscle in the gorilla and chimpanzee, but in the orang it tends to become fused with

FIG. 13.—Thigh of Rhesus monkey (*Macacus rhesus*). *a*, presemimembranosus ; *b*, semimembranosus ; *c*, pectineus ; *d*, adductor longus ; *e*, adductor magnus ; *f*, obturator nerve ; *g*, femoral artery ; *h*, ilio-psoas.

the adductor mass as in man. The insertion of the semimembranosus in the lower mammals is much less complicated than it is in man: the tendon, instead of being chiefly inserted into the back of the internal tuberosity of the tibia, passes deep to the long internal lateral ligament of the knee, and is inserted

into the antero-lateral part of the tuberosity (figs. 13 and 14). In man there is an expansion from the main insertion, which runs forward deep to the internal lateral ligament, and this expansion

FIG. 14.—Thigh of *Lemur brunneus*. *a*, sartorius; *b*, semimembranosus; *c*, internal lateral ligament; *d*, gracilis; *e*, semitendinosus; *f*, adductor; *g*, vastus internus.

is the remains of the original insertion. The new insertion in man into the back of the internal tuberosity is the result of the change in the usual position of the knee from flexion to

extension. The other expansions of the semimembranosus tendon to the posterior ligament of the knee and to the popliteal fascia, which are so well seen in man, are only found in a very rudimentary condition in the higher apes, and not at all in other mammals.

Semitendinosus.—This is a very constant muscle in mammals: it normally has one head of origin from the tuber ischii, and another from the anterior caudal vertebræ. These two heads unite in the upper part of the thigh, and where they unite there is very commonly a tendinous intersection. In the great anteater (*Myrmecophaga jubata*) the two heads remain as distinct muscles to their insertion. Neither of them has a tendinous intersection.

The insertion is into the cnemial crest of the tibia, just below that of the gracilis, with which it occasionally blends, especially in lemurs (fig. 14). The tendinous intersection often marks the union of the two heads of origin, but I cannot think that this is sufficient to explain its existence, since a tendinous intersection is not always, or even often, formed where two fleshy heads of a muscle join. It is, on the other hand, difficult to believe that the intersection is of the same morphological value as those in the rectus abdominis: if it be a myocomma it is, as far as I know, the only instance of such a thing to be found in the extremities. I am unable to understand the meaning of the structure, and can only bring forward evidence as to its frequent appearance throughout the mammalia.

Adductor cruris (Gracilis).—This muscle in the rodents and insectivores is often double, though this is never the case in the carnivores, lemurs, or monkeys (fig. 15). When it is double, the anterior part rises from the ilio-pectineal line and anterior (cephalic) portion of the symphysis pubis; it is inserted into the patella and ligamentum patellæ. The posterior part, or gracilis accessorius, as it is sometimes called, rises from the posterior (caudal) part of the symphysis and the subpubic ramus, and is inserted into the cnemial crest of the tibia. When there is only a single muscle, its attachments correspond to those of the last described; and I would therefore suggest that the anterior of the two is more worthy of the name of adductor cruris accessorius, or gracilis accessorius.

Tibialis anticus.—The *tibialis anticus* is usually regarded by anatomists as the serial homologue of the extensor ossis metacarpi pollicis of the anterior extremity, and its insertion certainly leads one to this view: comparative anatomy, however, suggests that the muscle may originally have had a femoral origin, and that the proximal part of it may correspond to the radial extensors of the carpus. In some of the ungulates, *eg.*, the horse and the pig, it rises from the front of the lower end of the

FIG. 15.—Leg of Guinea pig (*Cavia cobaya*). *a*, anterior gracilis; *b*, posterior gracilis.

femur. I have found the same origin in the agouti (*Dasyprocta cristata*), the paca (*Coelogenys paca*), and in two guinea-pigs (*Cavia cobaya*) out of five (fig. 16), while Mivart, Beddard, Windle, and Manners Smith have also found it in other animals belonging to the rodent families of *Dasyproctidæ* and *Caviidæ*.

Testut states that a femoral origin has been found once or twice in man, but I can find no record of it in any of the other primates.

The insertion is into the entocuneiform and base of the

first metatarsal whenever these bones are present. When the first metatarsal is suppressed the tendon shifts its attachment to the second, and in the horse to the third. In most monkeys and apes the tarsal and metatarsal insertions are separate in the lower part of the leg and foot, and in some cases form two perfectly distinct muscles. As far as I know, this arrangement is only found among the primates.

Extensor longus digitorum.—The typical origin of this muscle in mammals is by a tendon from the front of the outer

FIG. 16.—Leg of Guinea pig (*Cavia cobaya*). *a*, tibialis anticus (femoral origin); *b*, tibialis anticus (tibial origin); *c*, extensor longus digitorum; *d*, peroneus longus.

condyle of the femur (fig. 16), and its insertion is, as in man, into the middle and distal phalanges of the four outer toes when they are present. This description applies to the rodents, carnivores, insectivores, ungulates, some edentates, and many bats. In monotremes and marsupials the origin is usually from the fibula, but I have dissected two kangaroos in which, although the muscle rose chiefly from the fibula, a delicate ligamentous origin could be traced up to the external condyle of the femur. My present knowledge makes me regard carnivores, insectivores,

and rodents as furnishing better clues to the primitive arrangements of muscles than either marsupials or monotremes. In many edentates and bats, and in all the primates, the muscle has only a fibular origin. I am totally unable to suggest any similarity in the use of the hind-limbs of monotremes, marsupials, edentates, lemurs, monkeys, and man that could account for the slipping down of the origin of this muscle from the femur to the fibula.

Peroneus tertius.—This is always regarded as an essentially human muscle, though it occasionally appears in the anthropoid apes. In a three-toed sloth (*Bradypus tridactylus*) I found that the extensor longus digitorum, instead of going to the toes, was inserted into the bases of the inner and outer of the three metatarsal bones: the outer of these insertions would be practically homologous with the peroneus tertius of man. It is very well known that in man a slender tendon often runs forwards from the insertion of the peroneus tertius to join the extensor tendon of the fifth toe on the dorsum of the proximal phalanx: this slip is usually regarded as a remnant of the peroneus quinti digiti, with which it accurately agrees in position. It is, however, just as likely that it represents part of the extensor longus digitorum to the fifth toe, running forward from the point where that muscle acquires an attachment, to the base of the fifth metatarsal bone.

Peroneus longus.—This muscle always arises from the head and upper part of the shaft of the fibula, as well as often from the external tuberosity of the tibia and the external lateral ligament of the knee. In some animals, *e.g.*, hyæna, coati, badger, and mole, it is said to take origin from the external condyle of the femur, though it certainly did not do so in the hyæna, coati, or mole which I examined; indeed, I have never seen this muscle rising from the femur, though I have often done so from the external lateral ligament: such good observers, however, have described a femoral origin that I cannot doubt its occasional occurrence. In the carnivora, insectivora, and rodents the tendon passes through a separate groove, not behind but on the outer side of the external malleolus; it then runs across the sole, to be inserted into the base of the innermost metatarsal bone, and often the internal cuneiform. In the liter-

ature of this muscle it is very common to find records of its partial or complete insertion into the cuboid or outer metatarsals: it should be borne in mind, however, that it is quite easy to mistake the attachments of the sheath of the tendon for those of the tendon itself.

Peroneus brevis.—The peroneus brevis is a very constant muscle in rodents, carnivores, insectivores, and primates. It always arises from the fibula below the origin of the peroneus longus, and is inserted into the base of the fifth metatarsal bone (fig. 17). It occupies a groove behind the external malleolus, in common with the peroneals of the fourth and fifth digits. In the pig the muscle is said to be inserted into the second phalanx of the fourth toe, while in the horse it is described as the only peroneal present, and joins the common extensor tendon on the dorsum of the foot. In some of the more specialised hystricomorphine rodents, such as the agouti (*Dasyprocta*) and the Patagonian cava (*Dolichotis*), in which the fifth toe is suppressed, the muscle is wanting.

Peroneus quarti digiti.—This muscle in the more generalised orders (rodents, insectivores, carnivores, and primates) arises from the fibula a little lower than the origin of the peroneus brevis (fig. 17); it passes through the same groove behind the external malleolus, lying on the inner (mesial) side of that tendon. Its insertion is into the extensor tendon on the fourth toe. Among the above-mentioned four orders the muscle is only absent, as far as I know, in the tree porcupines (*Sphingurus* and *Erethizon*) and the higher primates. It is always present in lemurs, occasionally in cynomorphous monkeys, rarely in anthropomorphous monkeys, and never in man.

Peroneus quinti digiti.—When all four of the true peroneals are present, and among these the peroneus tertius is not included, the peroneus quinti digiti rises from the fibula, rather above the origin of the peroneus brevis. It passes through the same groove as the brevis, behind the external malleolus, and lying on the outer side of that tendon (fig. 17). In the foot it joins the slip from the extensor communis to the fifth toe. The peroneus quinti digiti is present in most animals which have a fifth toe; it is absent in a few hystricomorphine rodents, in most ungulates except the pig, and in the higher primates. With regard to the primates,

the muscle is always present in the cynomorpha, while in the anthropomorpha it is fairly often seen as a slip from the peroneus brevis tendon: this is the condition in which it is often found in man (58 per cent.—Gruber), and I cannot help believing

FIG. 17.—Leg of *Lemur branneus*. *a*, peroneus brevis; *b*, peroneus quinti digiti; *c*, peroneus quarti digiti; *d*, peroneus longus; *e*, extensor brevis digitorum; *f*, rotator fibulæ.

that when, in man, a slip from the peroneus brevis passes to the dorsum of the fifth toe, that slip represents the distal part of a peroneus quinti digiti, but when a slip passes from the peroneus

tertius to the dorsum of the fifth toe, it represents the distal part of some of the extensor longus digitorum, the proximal part of which is the peroneus tertius.

Gastrocnemius.—It is very well known that in man the outer head of the gastrocnemius arises from the outer side of the external condyle, while the inner comes from the upper and back part of the internal condyle; this arrangement holds good for most

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FIG. 18.—Tendo-Achillis of Beaver (*Castor canadensis*).

mammals, and is especially accentuated in those which progress by leaping; for instance, in both the kangaroos (*Macropus* and *Petrogale*) and the Cape jumping hare (*Pedetes caffer*) the external head has an origin from the outer side of the patella. Fabellæ are present in the heads of the gastrocnemius in most mammals with functional hind-limbs, except, perhaps, the ungulata; the outer one is always the best developed, while the inner one is often found in adult or old animals. In the Collective Investigation Report of the Anatomical Society for 1897, it was found that sesamoid bodies (fabellæ) of some structure occurred in about 28 per cent. of outer heads of the human gastrocnemius, and in about 13 per cent. of inner heads. They are occasionally ossified in the outer head, but very rarely in the inner. Some time ago I pointed out in the *Journal of*

*Anatomy*¹ that the component parts of the tendo-Achillis, even in man, were twisted in a rope-like manner, and that the fibres of the inner head passed superficial to those of the outer, and eventually gained the outer side. This arrangement can be very well seen in the beaver (*Castor Canadensis*), in which animal the two heads remain distinct as far as their insertion (fig. 18). Further experience convinces me that the arrangement is very general throughout the mammalia, though I do not know of any satisfactory explanation of it (fig. 19).

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FIG. 19.—Tendo-Achillis of Ruddy Ichneumon (*Herpestes smithi*).

Soleus.—The typical mammalian arrangement is for this muscle to rise from the back of the head of the fibula, and to be inserted into the inner part of the tendo-Achillis. Sometimes, as in the mole, it has a small origin from the tibia, but as a rule no

¹ Vol. xxviii., p. 414.

important tibial attachment occurs until the higher primates are reached. In many kangaroos, as well as the families of the Hyænidæ and Canidæ and the otter among the carnivora, the muscle is wanting. In the ungulata it is extremely rudimentary, while in the pig it is said to be absent by Meckel, though Lesbres thinks that it has shifted its origin to the femur, and has become fused with the external head of the gastrocnemius. In the lemurs and cynomorphine monkeys the muscle has the typical mammalian arrangement, but in the anthropomorpha origins from the tibia are frequently found foreshadowing the extensive tibial origin in man. This powerful tibial attachment is, I think rightly, looked upon as one of the most important muscular changes brought about by the upright position.

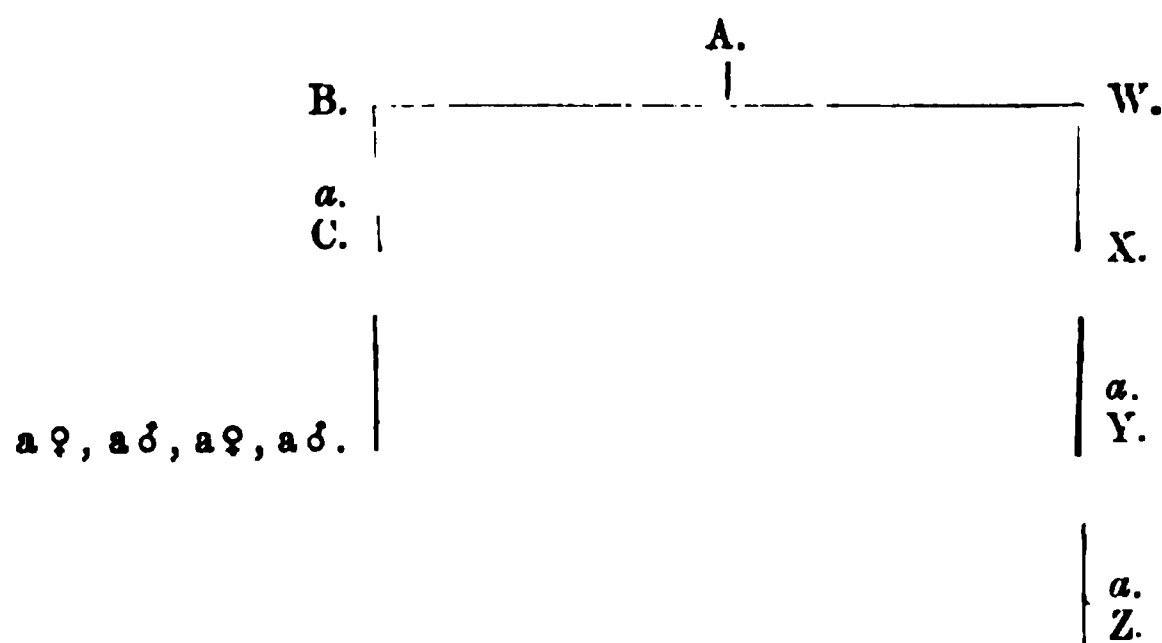
Plantaris.—Just as the soleus is in a progressive condition in man, so the plantaris is retrogressive. In almost every mammal it is found as a large muscle arising from the back of the external condyle, and winding round the inner side of the tendo-Achillis to reach the superficial aspect; it then passes round the projection of the heel, and instead of being inserted into the calcaneum as in man, is continued into the sole, and divides into two layers, the superficial of which is the plantar fascia, and the deep the flexor brevis digitorum. The plantar fascia can be traced to the proximal phalanges of the toes, the flexor brevis to the middle phalanges, and it would thus seem that in mammals the plantaris is a flexor of both these sets of bones; there is, however, good reason for thinking that the flexor brevis digitorum is really a continuation of the soleus which has lost its connection with that tendon, and acquired a new one with the plantaris on account of the hyperextension of the ankle joint, and the marked prominence of the tuber calcis. As we approach the higher mammals, we find that the cheiroptera are remarkable for the absence of the plantaris, but in lemurs the typical mammalian arrangement exists. Keith points out that this is also the case in the cynomorphous monkeys, but in the Anthropomorpha the muscle is rarely seen in gorillas, oranges, and gibbons; it is present, however, in about 75 per cent. of chimpanzees. In man the plantaris is present in about 90 per cent., according to the Anatomical Society's Collective Report for 1894.

A NOTE ON HEREDITARY STIFFNESS OF THE METACARPO-PHALANGEAL JOINT OF THE THUMB.

By J. H. F. WILGRESS, Selwyn College, Cambridge.

THIS abnormality consists in the complete absence of all voluntary movement of the joint in question: the phalanx could, however, be forcibly flexed to a small extent, through an angle of not more than 10° , the normal angle of flexion being 50° to 68° . The extensor tendons in both hands of all the individuals referred to who were examined, were found to be present.

The peculiarity was observed in the individuals of three generations, but the fact that it was present in two different branches of the same family tended to show that it had possibly descended through five generations at least, as the common ancestor of the two branches was separated from the youngest member who had the abnormality by three generations. A. had two sons, B. and W. B. and W. had sons C. and X.; the metacarpophalangeal joint of the thumbs of C. were stiff. C. had seven children, of whom two males and two females had the abnormality in both hands. X. had a son Y.; Y. had a son Z. both Y. and Z. had the abnormality in each hand.



a. denotes those members who had the abnormality.

The hands of A., B., W., X. were not available for examination.

ON SOME SKULLS FROM CEYLON. By EDRED CORNER,
M.B., B.Sc., Sidney Sussex College, Cambridge.

THROUGH the kindness of Dr Rockwood I received six skulls from Colombo, Ceylon: two of these were Tamils, two Singhalese, and the others Moor.¹ Besides these, I have measured one Singhalese and a Veddah skull which are in the Cambridge Museum.

The Tamils and Singhalese have been carefully studied by the brothers Sarasin (19), but they had described no specimen of the Moors. On consulting the literature, I have been unable to find any description of the crania of the last. Tennent (8), vol. i. p. 605, says: "The most remarkable of the many tribes which inhabit Ceylon are the Mahommedans, or as they are generally called, Moormen. They are found on all parts of the coast, and their origin, arrival, etc., are amongst the historical mysteries of Ceylon." He says that these Arabs were at Ceylon before the Portuguese arrived, and from them the Moors have descended. The Singhalese name—*marak kala minisu*—means mariners, and refers probably to their origin. Swamy (14) mentions the Moors as part of the Asiatic population of Ceylon, and says that they are the small traders and shopkeepers of the island.

Ramâthan (20) has an interesting paper on the ethnology of the Moors. Quoting the census of 1881, he shows that they form an enormous proportion of the Mahommedan population. By the language of the law courts they are divided into two sections,—the first, or Ceylon Moormen, who were the earlier arrivals; the second, or Coast Moormen, came later by boat from India. He says they are nearly all Tamil-speaking Moham-medans. They resemble the Tamil in physique, speak the Tamil language, have no craniological distinction from them (criticising Virchow), and their history derives them from the Tamil.

Bawa (21), in the same Journal, gives an interesting account

¹ These skulls are now in the Cambridge Museum.

of their marriage ceremonies. Sarasin (19) gives an account of the external characters of the Moors, which differ little from those of the Tamil. He thinks that they have originated from the Arabs. Risley (32) gives the cranial and other measurements of twenty-two living Moors, and contrasts them with those of 56 Tamil and 56 Singhalese.

As regards the relations of the Tamil and the Singhalese, the Sarasins regard the Tamil as being nearer the Veddahs than the Singhalese are. The last, they think, have more Aryan blood in them than the Tamil, and this constitutes the great difference between them. Wevill (31), p. 38, gives the divisions of the Tamil, Singhalese, and Veddah into their ethnic portions. Both Virchow (18) and Risley (32) give some measurements taken on the living subjects.

The following is a description of the skulls now in the Cambridge Museum:—

1. Singhalese. Punchi Appoo, from Waharampitiya; male; age 40. A moderate-sized, phænozygous, and symmetrical cranium, with two supralambdoid wormian bones, also accessory bones in the lambdoid suture, a left epipteris bone, and small ossicles in the coronal suture. The forehead is somewhat receding, and there is a slight metopic ridge present. The groove for the middle and temporal artery is well marked on both sides. The palate is deep, the paramastoid processes large, and the glenoid cavity more than ordinarily sunken. When looked at in *norma occipitalis*, there is some indication of symmetrical flattening just above the asterion, which is well seen in the Veddah skull.

In the lower jaw the genial tubercles are large.

2. Punchi Mona, from Waharampitiya; female; age 35. This is probably younger than the age given, as the last molar tooth on both sides is not fully developed. It is symmetrical and phænozygous, with simple sutures, and a wormian bone present in the lambdoid suture. The groove for the deep temporal artery begins in front of the external auditory meatus, and not, as in the preceding specimen, somewhat behind it. A slight depression exists above the lambda, and also behind the coronal suture. The left infraorbital foramen is double. The palate is highly arched.

3. A male skull, No. 1197 in the Cambridge Collection.

The contour is symmetrical, and it is phænozygous. The sutures are simple, with some synostosis about the obelion and below the stephanion. The sagittal suture is slightly raised on a ridge, and the parietal eminences are prominent. Behind the coronal suture is a depression. There is a large patch of carious bone on the frontal. The muscular markings are large and rough, and the external occipital protuberance is very prominent. Ossification of the pterygospinous ligament has taken place, and the plate of bone thus formed is pierced by several foramina. The palate is deep, as in the other Singhalese skulls. The groove for the middle temporal artery begins just above the meatal spine, which is large, and proceeding upwards and backwards, ends in several branches near the inferior temporal line.

On the right side the zygomatic suture is obliterated, and on the left only the upper part is synostosed. Wormian bones are present in the lambdoid suture.

4. Tamil, named Weenappan, from Eingenada; male; age 37. A symmetrical and phænozygous skull, with simple sutures, and a wormian bone in the lambdoid suture. On the under surface of the petrous bone, and just anterior to the entrance of the carotid canal, is a large process. This seems to be correlated with smallness of the spine of the sphenoid. The glenoid cavity is deep, as is also the palate. A slight post-coronal depression is present. Three well-marked foramina are seen on the molar bones. In the upper and posterior part of the bony ring of the external auditory meatus is seen a large meatal spine.

5. Tamil, named Muttanuna, from Palamcotta; age 40; female. The surface of the bones is rough; the sutures, which are simple, with wormian bones in the lambdoid, are placed on ridges. As in the preceding specimen, it is symmetrical, and just phænozygous. A ridge marks the place of the metopic suture. The groove for the deep temporal artery begins just above the right meatal spine, which is especially large: on the left side it begins in front of the external auditory meatus, and is shorter. A very large fossa exists over the posterior condylar foramen. The palate is high.

At the lower part and on either side of the symphysis menti is a sharp bony process. The meatal foramina are large. Ossifica-

tion has evidently extended into the tendons attached to the genial tubercles, as these are enormously enlarged.

6. A Moorman named Sacthan, from Colombo; male; age 48.

A symmetrical phænozygous skull, with simple sutures, and a wormian bone in the lambdoid suture near the right asterion, and with a rough surface. The groove for the deep temporal artery is extremely well marked, and extends from the meatal spine upwards and backwards as far as the inferior temporal line, where it ends in many branches, most of which run forwards. The temporal lines show a very considerable post-stephanic rise, the shortest distance (chord) between the two superior temporal lines being 55 mm. (*Jour. Anat. and Phys.*, vol. xxx. p. 382). The paramastoid ridge is especially large on the right side, as is also the superior curved line of the occipital bone.

7. A Moorman named Abdulla, from Slave Island; male; age 42.

A large symmetrical, phænozygous skull, the sutures of which are fairly simple and tend to be situated on ridges, especially the coronal. Accessory bones are present in the lambdoid suture. Slight synostosis has occurred near the obelion. On the parietal (left) and frontal bone are three or four areas of superficial necrosis. Slight flattening is seen just above the lambda.

On the lower jaws of both these specimens the genial tubercles are especially large.

8. Veddah, No. 1196; male; age about 22; probably female.

The skull is smooth, small, symmetrical, and phænozygous, with very simple sutures. A large number of accessory bones are present, viz., two supralambdoid, one lambdoid, and epipteric bones on both sides. Depressions exist above the lambda and behind the coronal suture. A metopic ridge is present. The palate is not so deep as in the other skulls; no prenasal fossæ are present. Both deep temporal grooves are small. In the left orbit there is a trochlear spine.

The alveolar processes of the upper jaws are very short, the depth measuring only 12 mm. The following table shows the same measurements in the other specimens:—

Singhalese,	20, 21, 21·5 mm.
Tamil,	24, 23 mm.
Moor,	22, 16 mm.
Veddah,	12 mm.

On examining the skull in *norma occipitalis* it will be noticed that the greatest breadth is between the parietal eminences. Behind the asterion is a marked depression, making the occiput somewhat bullate; this depression is continued forward above the asterion, so causing the diameter here to be less than the biparietal or bimastoid. This gives a peculiar appearance to the skull when seen from behind.

Bimastoid,	116 mm.
Biparietal,	123 mm.
Breadth at depression,	112 mm.

The nasal opening in the Veddah skull is *oxycraspedote*, bounded by the sharp lines of the lateral margin and the paraseptal line, which were confluent. The nasal spine was broken.

Two of the Singhalese exhibited the *foetal amblycraspedote* condition, where the lateral margins and paraseptal lines do not meet, giving a rounded border. The other was *bothrocraspedote*, with a prominent anterior dental ridge. All these were *oxyacanthic*.

Of the Tamils, one was *amblycraspedote* and *oxyacanthic*, and the other *bothrocraspedote* and *lophacanthic*, the nasal spine projecting but little. The Moors were both *amblycraspedote* and *oxyacanthic*. These results entirely bear out Prof. Macalister's statement of the relations of these conditions with *orthognathism* and *microdontism*.

These crania present a few anatomical points deserving of special note. In a Tamil skull a process has developed from the petrous bone that apparently replaces the very small sphenoid spine. One Singhalese skull shows the ossification of the pterygospinous ligament. Prof. Charles (*Jour. Anat.*, xxvi. p. 1 and xxvii. p. 5) noticed that supplementary bones occurred in 64 per cent. of Indian crania, and I found them in 70 per cent. of a series of crania from the N.W. Provinces of India (*Proc. of the Camb. Phil. Soc.*, vol. viii., pt. v., p. 287). In the eight skulls now examined they are present in every one. Another noteworthy point is the very large genial tubercles found in the lower jaws.

The following tables show the relations of the average indices obtained from the literature and those obtained from the skulls that form the subject of this paper:—

Singhalese.

Number.	Cap.	Cephalic.	Vertical.	Gnathic.	Nasal.	Orbital.	Author.
9	1345	72·5	73·9	99·2	50·6	83·7	Sarasin.
3	1249	71·3	73·4	96·3	54·9	81·7	E.C.

Tamil.

13	1336	70·8	73·6	98	52·5	86·7	Sarasin.
2	1210	73·1	73·5	96·7	54·1	82·7	E.C.

Moor.

2	1399	73·9	77·7	93·9	54·1	82	E.C.
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In the living subject, both Risley's and Virchow's results are given in the following table:—

		Cephalic.	Nasal.	Nasomalar.	Author.
Singhalese—	4 males, .	78·3	Virchow.
	2 females, .	81·0	„
	Both together,	79·2	
	56 males, .	78·3	82·7	113·0	Risley.
Tamil—	56 males, .	77·7	83·6	111·4	„
Moor—	22 males, .	79·1	80·7	111·6	„

It will be seen that the indices of all three varieties of skull, both in the Sarasins and my series, agree closely. Again, the results of Risley and Virchow's measurements show that there is little difference to be found in their measurements in the living.

If these crania are defined in series of their indices, they are all dolichocephalic and metricephalic (except one Moor, which is just akrocephalic). Sarasin makes the Tamil and Singhalese mesognathous; but all in this series are orthognathous except one Tamil, which is mesognathous. Similarly, Sarasin's series are mesorhine, and this is just platyrrhine. All are microseme except one Tamil, which is mesoseme. In respect of capacity, both the Tamil and Singhalese are microcephalic, the former being slightly the smaller. The Moors are mesocephalic, but one was macrocephalic (1523 c.c.). All are dolichuranic.

With regard to the nasomalar index of Oldfield Thomas, the Moors are markedly prosopic (114·7) and the Singhalese barely so (110·5), whilst the Tamil are just within the mesopic class (109·5), and the Veddah (105) is platyopic. In this case Sarasin's

opinion that the Tamils are nearer the Veddah than the Singhalese is borne out, but only by a very little. The prosopy of the Moor confirms their probable Arab origin.

Neither the facial indices (both Kollmann's and Virchow's) nor Topinard's index help us in separating the groups. All the skulls are phænozygous.

To sum up, therefore, the characteristic points indicated by the study of these two Moor skulls, they are a heavier, more massive, more strongly marked, are higher, have a greater cranial capacity, and are more markedly prosopic. Beyond these points nothing can be said, for the figures quoted show their proximity to the Singhalese and Tamil; similarly, they also show the close relationship of these last two groups to each other.

TABLE I.—Measurements.

Capacity.	1195	1415	1130	1125	1295	1275	1523	1130
Frontomalar Arc.	100	112	95	102	110	108	112	95
Horizontal circumference.	477	517	470	485	510	490	528	470
Sagittal circumference.	560	572	530	540	573	565	594	530
Nasion-alveolar	490	508	473	488	499	498	525	473
Nasion-basion Arc.	398	405	388	390	402	407	423	388
Nasion-opisthion Arc.	366	367	349	351	362	366	384	349
Nasion-inion Arc.	313	324	312	310	315	307	338	312
Nasion-lambda Arc.	262	260	250	245	255	257	268	250
Nasion-bregma Arc.	131	127	127	120	130	126	135	124
Biasterial.	91	108	108	97	108	97	111	93
Elstephanic.	106	113	109	100	101	118	120	101
Mentonasal.	99	114	..	114	111	104	116	..
Interorbital.	19	23	24	23	18	24	22	20
Palate.	Length.		Breadth.					
	60	63	67	66	59	59	65	53
Orbital.	Height.		Breadth.					
	36	40	41	38	2	39	40	36
Nasal.	Length.		Breadth.					
	22	27	27	25	24	25	27	22
Minimum frontal.		87	94	98	90	91	99	87
Frontomalar.		89	102	105	93	99	98	90
Bimaxillary.		92	98	95	97	85	98	84
Bizygomatic.		110	129	130	117	125	136	114
Nasioalveolar.		59	66	68	62	72	70	56
Basialveolar.		94	101	99	101	99	102	86
Basinasal.		95	107	104	100	107	112	91
Basibregmatic.		130	129	137	129	135	146	130
Breadth.		127	134	125	132	131	139	123
Ophryo-occipital.		171	179	182	174	185	186	170
Length.		171	186	184	175	185	188	170
Sex.		F.	M.	M.	M.	M.	M.	M.
Age.		35	40	..	37	40	42	22
Singhalese,								
Singhalese,								
Singhalese,								
Tamil,								
Tamil,								
Moor,								
Moor,								
Veddah,								

TABLE II.—Measurements.

	JAW MEASUREMENTS.							INDICES.						FACIAL INDICES.				Capacity.	Topinard's Index.
	Sex.	Age.	Mental Height.	Condylar Height.	Bicondylar Width.	Biangular Width.	Depth.	Weight in Grammes.	Cephalic.	Vertical.	Gnathic.	Nasal.	Orbital.	Palatine.	Kollmann's Upper.	Kollmann's Total.	Virchow's Upper.	Virchow's Total.	Nasomalar.
Singhalese,	F.	35	20	58	99	90	78	66	74.2	76	99.4	52.3	L.86.1 R.83.3	86.6	53.6	90	64.1	108.8	112.3
Singhalese,	M.	40	35	63	104	91	82	75	72	69.3	94.3	56.2	77.7	97	51.1	88.3	67.3	116.3	109.8
Singhalese,	M.	..	38	67	114	97	80	73.5	67.9	75.0	95.2	56.2	82.9	89.5	52.9	97.4	71.5	117.5	109.6
Tamil,	M.	37	35	59	111	95	83	79	75.4	74.2	101	60.9	88.8	85.9	57.6	88.8	63.9	130.5	111.1
Tamil,	F.	40	35	61	109	93	86	76	70.8	72.9	92.5	47.2	L.78.5 R.75.6	94	49.2	83.8	84.6	107.2	108
Moor,	M.	48	23	71	113	97	80	73	73.9	77.8	96.8	64.3	L.84.6 R.79.4	94.0	50.8	85.2	62.8	115.3	114.2
Moor,	M.	42	35	67	117	108	85	72	73.9	77.6	91.0	64	80	95.3	52.3	..	71.4	..	115.2
Veddah,	72.3	76.4	94.5	60	83.3	86.8	49.1	..	66.6	..	106.5

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SOME NOTES ON THE MANUS OF THE DUGONG.

By RICHARD J. ANDERSON, *Professor of Natural History,
Queen's College, Galway.*

THE Dugong, of which there are three species, lives on the shores of the Indian Ocean and the Red Sea. The scapula measures, in the specimen under consideration (Halicore — ?), 11 inches; the humerus, 7·2 inches; the radius, 5·2 inches; and the wrist and hand, 7·2 inches. The humerus is complete as the epiphyses are united with the shaft; the radius and ulna are free; their upper ends are complete, but the lower epiphyses are still separated from their respective bones, and are not united with one another to form a single bone, as in the Manatee; and the shafts of the radius and ulna are free in their whole length.

The upper wrist bones are two (scapho-lunar and cuneiform), and there is only one lower wrist bone. The fusion of the carpalia, a common thing in the Dugong, reminds one of the lenticular bone at the ulnar side of the wrist in the Crocodile.

The metacarpal bones, five in number, have the following lengths:—

Left Arm:—I., 2½. II., 3. III., 3½ IV., 3½ V., 3—
(all inches).

The distal epiphyses are still separate.

In the right manus the lengths are the same, with the exception of the third, which, having lost its distal epiphysis, is reduced to 3 inches.

The first phalanges differ in epiphysial arrangement from the condition which exists in Man, where, as is well known, the epiphyses are proximal in the four ulnar digits; the first forming an exception. The lengths are in inches—

I., absent. II., 7⁄8. III., 1¼. IV., 1½. V., absent.

II., III., and IV. have both proximal and distal epiphyses. The epiphyses of the fourth remain separate. Those of the second and third are partially ankylosed to their respective shafts.

In the right hand the measurements are—

II., $\frac{5}{8}$. III., $\frac{7}{8}$. IV., $1\frac{1}{8}$. V., $\frac{3}{4}$.

The epiphyses here were mislaid or lost in the case of the second and third. The shortening is thus accounted for, whilst the caps are retained on the fourth, and have been likely lost in the fifth.

The arrangement here differs from that of many animals, and conspicuously from the condition in Man.

The second phalanges on the left hand measure in inches—

II., $\frac{3}{8}$. III., $\frac{7}{8}$. IV., 1 inch.

The proximal epiphysis in II. is doubtful; in III. it has been lost; and in IV. it is partially ankylosed. There are no distal epiphyses. The measurements on the right are—

II., $\frac{1}{2}$. III., $\frac{3}{4}$. IV., 1 inch. V., $\frac{5}{8}$.

The epiphyses of II. are imperfectly distinguishable. III. retains its proximal epiphysis. In IV. the proximal epiphysis has been lost. V., neither of the epiphyses remain.

In the third phalanx the measurements are—

Left:—III., $\frac{1}{2}$. IV., $\frac{5}{8}$.

There is evidence of the existence of a proximal epiphysis on IV., and *perhaps* a distal epiphysis.

Right Manus:—III., $\frac{1}{2}$. IV., $\frac{5}{8}$ (all in inches).

Proximal epiphyses present on IV.; distal, 0.

The fifth metacarpal articulates, of course, with the cuneiform.

The Manatees that frequent the shores of the Atlantic are distributed into two or three species that are said to like the land better than the Dugongs. It is interesting to note the peculiarities of the manus as compared with that of the Dugong, which most appropriately lacks nails that the Manatee possesses and requires.

The upper articular ends of the humeri are not united with the shaft in the specimen examined, and the tuberosities are incompletely ankylosed. The lower epiphysis of each is joined to the shaft.

The radius and ulna are completed by the ankylosis of their epiphyses, and the heads of the bones are, further, joined together at the elbow.

The wrist ends are separate, and joined to one another on the left side; not joined on the right side. The wrist itself has six bones: the pisiform is absent. Three form the upper and three the lower row. Metacarpal V. articulates with the ulnar element of each row.

The metacarpals of the left manus have the distal epiphyses still separate on III., IV., and V. The remaining joints have no discernible epiphyses.

The third phalanx of the index finger is ankylosed to the second.

In the right manus, the epiphysial caps at the lower end of the radius and ulna are separate from their respective bones and one another. Metacarpals III., IV., and V. have distal epiphyses, all ununited. The distal phalanges of ring and index are ankylosed to the second phalanges of the same fingers.

It will be seen that, whilst the free bones in the wrist are more numerous in the Manatee than in the Dugong, the bones of the Dugong hand are freer than those of the Manatee.

The epiphyses of the seal have been noted. The metacarpals have distal epiphyses: the first a proximal, and the phalanges distal in *Halichoerus grypus*.

A peculiarity in the manus of the Indian elephant has been noted. The metacarpal of the pollex has separate epiphyses at its two articular ends. This is of interest in discussing the homology of the metacarpal bone of the thumb. The remaining metacarpals have distal epiphyses only; and the phalanges, proximal epiphyses.

The right pes of the young elephant examined (which was 6 feet high at the shoulder) did not show this peculiarity. The first metatarsal has a proximal, but no distal epiphyses. The epiphyses of the remainder are normal.

SOME POINTS CONCERNING THE MOUNTING OF
DISSECTIONS IN BASINS. By EDWARD FAWCETT,
M.B. Edin., *Professor of Anatomy, University College,
Bristol.*

EVERYONE who has had charge of an anatomical museum has probably found that 'basin-preparations' are more or less a nuisance from the time they are mounted, and even before that. The question of expense is in many cases an important one, although basins, effective in every respect, can be obtained at a very low price. Many makers of earthenware goods, however, fight shy of making anything out of the common, as doubtless many anatomists have found. If the worst come to the worst, the ordinary glass basin, which can be got from various dealers, with wide flat rim, answers perfectly well, and I know of nothing which looks neater. I described in the *British Medical Journal* of 1894 a form of basin in earthenware which I have found perfectly satisfactory. These basins were circular in form and had a flanged upper rim. Since then I have had made for me several rectangular basins, large enough to hold the forearm and hand, in white glazed pot with flanged rim, which not only serve the purpose admirably, but look extremely well. I am partial to the flanged rim, although it is not absolutely necessary. These latter basins are made at a very low price, and I shall be glad to answer any inquiries made in respect of them.

The Cover.—The cover one generally sees is thick plate glass. This is expensive, and is by no means necessary. Sheet glass one-eighth inch in thickness answers every purpose: it is easy to drill, and is in every way less expensive.

The Cement.—This has hitherto proved the chief stumbling-block. It is usual to see in museums the cover fixed down with either gold-size and litharge (or red lead) or some preparation of caoutchouc.

The former answers well enough sometimes if properly mixed,

and if the surfaces to which it is applied be quite dry, but it is very difficult to be sure that it will not crack, when, of course, the basin springs a leak. It answers best with the flat-rimmed basin, and with preparations preserved in spirit.

The latter has the disadvantage of having to be applied hot, and there is besides a great risk of breaking the covers, without taking into account the horrible smell generated by heating it.

The cement which I have used for some time back I have found to be the most useful, most easily applied, and most trustworthy of any. That is a cement made by rubbing down on a slab of wood or metal, with the flat of a chisel, litharge and Archangel tar (used in caulking). As much litharge as will give an easily worked paste is used, and is conveyed to the basin and cover on the point of an old pocket-knife. If the rim of the basin be a flanged one—and this is the form I use—the cement is simply scraped in, like so much putty, between the glass and the flange; the interval between the edge of the cover-glass and the flange having been filled, enough cement is now used to fill up the angle between the top of the glass and the top of the rim, the cement covering the glass, say, for from a quarter to half an inch. This latter treatment is not absolutely necessary, as I have been able to prove, but it adds to the appearance, and certainly gives strength to the mount.

It is well now to allow the cement to stiffen, and if the right consistence have been got at first it will soon—in an hour or two—do that. The right consistence can be determined by pressing on the cement with a finger or thumb nail; if the nail do not easily make an impression, the cement is now ready to be treated with the hot file. I say *file*, because I have used an old triangular file whose point had been broken off, so that the end was now an equilateral triangle of from half to three-quarters an inch in side. Any other piece of metal of about the same width will do; I have used, with pleasing result, the loop of a latch-key. The file I have found convenient because, being thick, it retains the heat longer. This is heated in a Bunsen flame to avoid soot, and when short of red heat is run over the cement, one angle of the file being pressed through the cement down to the cover, the other resting against the inner edge of the top of the rim. The file is carried all round the glass, and soon the cement will become smooth on

the surface, and will be of stony hardness almost at once. With a pocket-knife any irregular patches of cement may be removed from the surface of the cover, and the operation is complete.

It is not necessary to use the file, but so satisfactory is the result in every way that I should not think of dispensing with it.

This process is simplicity itself, and with it basin work is a pleasure. The cement cannot crack, and in the summer it only becomes more elastic with heat.

This cement must not be used with spirit as a preservative, as it will soon be penetrated. Used with formaline, which seems to me to be an ideal preservative medium, for reasons which I will shortly mention, it seems to be perfect.

Other Cements.—I have been experimenting for the last five months with other two cements, both of which seem to be excellent. I have used them with the ordinary glass basin with flat rim—*i.e.*, having no flange. Up to the present no leakage has taken place; and as the cements have become harder, I have no particular reason for supposing that it will do so.

Both cements are 'proprietary' articles, and I am ignorant of their composition. Both have the great advantage of being liquid, and this saves enormous trouble. All cements which require to be heated are a nuisance, because unless the basin and cover can be heated too, the cement is half set before one can get half way round a basin.

One of these cements is called the 'Instant Crockery Mender,' the other is 'Seccotine.' The former is in bottle, the latter is in a leaden collapsible tube. I have not had so much experience with the latter. It is more convenient to use, as it can be squeezed on the rim as it is passed round, and an even covering can readily be got, whereas the former must be applied with a brush or knife, and it is difficult, without care, to ensure an even coating. On the whole, however, I at present incline to the former. Both are well worth trying. They are unsuited to spirit, and the parts must be dry.

Drilling the Cover-glass.—This is an operation usually left to the glazier, but it is so simple, and the necessary tools are so few, that any anatomical porter or museum assistant should be taught to do it.

The apparatus required consists of an Archimedean drill, a

few drill-points, a small saw-setter's file, and a little turpentine, and an ounce or two of mercury. Before the drill-points can be used they must be tempered.

To do this, a drill-point having been fixed in the drill, *its point* is held in the Bunsen flame till *yellow*; it is then plunged into a dish of mercury; and care must be taken to see that *only the tips* of the drill-point is plunged into the mercury, otherwise, if much of the shaft become as hard as the tip, it will be so brittle as to break when being used. If the temper be correct, the drill-point will now scratch glass, and it is ready for use.

A spot on the cover having been selected, the cover is laid flat on a *flat* table. A drop of turpentine is placed on the spot selected, and the drill, held vertically, is made to rotate. It soon 'bites,' and very soon embeds its head; as the dust works up from the hole, it may be removed, and the hole filled up with turpentine. The drill should not be very heavily pressed on, nor is it desirable to work it very quickly; for in the former case the glass may possibly crack, in the latter the drill may become hot and lose its temper. Plenty of turpentine will do much to prevent loss of temper.

It is astonishing how soon glass can be perforated in this way. I have drilled $\frac{1}{4}$ inch plate glass in less than ten minutes. But glass varies much in consistency, some being easily bored.

The hole having been made, presumably with a small drill-point, it may quickly be enlarged to such a size as required by the small triangular file. This should be set in a *cross piece* of wood, as a corkscrew is in its handle. Such a handle gives great power, and enables one to handle the file very delicately also. It is absolutely necessary to use turpentine during this operation. The file may be dipped in it, or the turpentine may be dropped into the hole,—it matters not which. The file is now rotated by the hand, complete rotation being desirable—hence the cross handle; and the glass gives way readily. If no turpentine be used, the glass will shiver, large pieces flaking off, and it may often crack. None of these accidents happen if turpentine be used.

The drill-points may become blunted during the operation, either from losing their temper through being rotated too quickly, or from being insufficiently tempered at the commence-

ment. They are easily sharpened. Heat them in the flame till red, then let them cool slowly. Rub them on the small saw-maker's file, keeping to the original bevels as far as possible. They readily become sharp, and can be at once re-tempered. After tempering, they can either be tested on the file if it be hard enough to scratch glass, in which case it will not touch the drills, or on glass itself.

Much time and expense are saved by drilling in this way.

The Preservative.—I now use weak solutions of formaline, having abandoned spirit entirely, for the following reasons:—Formaline does not penetrate the cement, it does not discolour, and so little is required of it. Spirit possesses none of these qualities. Nothing save the leaking of a basin is more annoying than discoloration of the preservative. The most beautiful dissections may look disagreeable under such circumstances. Many of my own specimens, especially dissections where many muscles were shown, had constantly to be attended to for this reason; but since the use of formaline and water they have required no attention whatever, for the fluid remains quite clear.

As the fluid tends to evaporate, it is best to cover the hole in the cover with a small thin cover-glass, such as is used with microscope slides; in fact, this is generally done. It may be fixed down with balsam or the cements I have mentioned—the tar-cement, of course, excepted.

As dissections are generally embedded in plaster of Paris, it may be well to say a word about it, when used with the ordinary glass basin.

Embedding in Ordinary Glass Basins.—Everyone knows that these thin glass basins readily crack during the 'setting' of the plaster. This may be avoided in two ways: either by layering the plaster in thin layers, which is very tedious, and as the sides of the basin are rarely vertical, the plaster, when once in, cannot, without very great trouble, be got out again; or, by a much simpler and absolutely safe method, which I shall describe at length.

Method II.—First procure some corrugated cardboard, such as is used by chemists for wrapping bottles in for transmission by Post, cut it to such a width as corresponds with the depth of the

glass basin, and to such a length as will completely line the interior of wall. A piece of brass wire may be made into a circle large enough to hold the cardboard against the glass wall, the ends of the brass wire overlapping one another, and being tied tightly by wire or string,—just so tightly that the circle can be enlarged or diminished by sliding one end on the other.

The cardboard may now be taken out, and the uncorrugated surface smeared all over with vaseline or thick soap jelly (the former is better). It is now replaced in the basin, the corrugated surface being outwards. The joint between the two ends is covered by a thin piece of paper, greased on both surfaces, in the one case to ensure adhesion to the cardboard, in the other, non-adhesion to the plaster, the ring of brass is fixed, and everything is ready for the plaster.

This can be poured in to any amount required; there is no danger of cracking the basin through expansion, as all that will happen, let the plaster expand to its utmost, is flattening of the corrugations. After the plaster is set, the cardboard can be removed either alone or with the plaster. In any case, the plaster can be lifted out of the basin with the preparation whenever required at any future time.

By this method glass basins can be used as readily as earthenware ones, and they look very neat; they are, moreover, cheap and easily obtained.

I might, perhaps, remark that these basins have the flat rim usually ground. I am not aware that this is necessary beyond ensuring a perfect fit, and it materially adds to the cost.

In this connection, I might also say that when using cements to fix covers down with, it is usual to place a weight on the cover. With the cements I have used, this, I feel, is a positive disadvantage. So far as my experience goes, it is rare to find the cover and rim fitting perfectly; if they do, there can be no harm in applying a weight; if they do not, and there is a slight tilting of the cover possible, it is far better to use plenty of cement, and let the cover find its own level by its own weight, because if it be weighted down and flattened in that way, it will tend to spring up when the weight is removed, and unless the cement be thoroughly hard throughout—and it is quite impossible to determine that—the glass will separate from the cement, and a weak

spot, if not a leak, may be the result, which will be an eyesore and a constant source of disquietude of mind.

It does not matter a straw how unequal the surfaces are when the 'tar-cement' is used; it will fill any gap, large or small. It does not matter either if the surfaces be not quite dry, and, more than that, if by any chance a glass have been fixed down by gold-size and litharge, and have begun to leak, after laying bare the leak it can be repaired with the tar-cement, the fluid all being displaced by the tar,—at least, such is my experience.

In conclusion, I may say that the tar-cement of which I have said so much was first devised by the anatomical porter at Leeds, and used by him to strengthen the gold-size and litharge cement which came into contact with the spirit preservative.

ARCHÆOLOGIA ANATOMICA.

I.

THE OLDEST ANATOMICAL MEMORANDA EXTANT.

THESE notes are contained in a papyrus in the Leipzig University Library, brought from Egypt by Professor Ebers in 1872. A facsimile of this document was published in 1875 by Professor Ebers, and translations of it have been made by Professor Lieblein and Dr Joachim.

The sections dealing with anatomy occur on pp. 99, 100–103 of the facsimile. The papyrus was probably written sixteen centuries before our era, as there occurs on the reverse of one portion a calendar written during the lifetime of King Amenhotep I. For the most part the work consists of notes or memoranda written by some ancient physician, and copied from still older medical writings.

The translation here given was made about ten years ago. I had intended to publish a version of the entire papyrus, but refrained, as so little could be definitely ascertained concerning a large number of the medicaments and prescriptions which make up the principal part of the book. Now that the contents of the work are accessible in the excellent and handy translation of Dr Joachim, the publication of any other rendering of it is superfluous until further light can be shed on the *materia medica* of the ancient Egyptian medical schools.

The anatomical notes embody rather a kind of traditional description than a record of exact observation. Such as they are, they are of great interest on account of their antiquity. I have not confined myself to an absolutely literal translation; but, while departing as little as possible from a faithful rendering of the original, I have tried to express in idiomatic English what seems to be the sense of the memoranda.—A.M.

BEGINNING OF THE BOOK OF MYSTERIES OF THE PHYSICIAN— THE KNOWLEDGE OF THE MOTIONS OF THE HEART—THE KNOWLEDGE OF THE HEART.

There are vessels from it to all the members. Each physician, master of healing,¹ priest-exorcist, feels all these when he places his finger upon the head, upon the scalp (neck or occiput), upon

¹ *Neb-secht*. Professor Ebers takes this as a proper name. See “Uarda.”
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the hands, upon the epigastrium, upon the arms or upon the legs. He traces all from the heart, because its vessels go into all his members, so he describes it (the heart) as the beginning of the vessels to all members.

There are four vessels to the nostrils, of which two carry fluid (mucus?) and two carry blood.

There are four vessels to the sides of the temples, which if they carry blood to the eyes, all manner of diseases are produced in the eyes by their means, by their being open to the eyes. If water flows from them, it is the pupils of the eyes which give it. It is otherwise said¹ that sleep causes it (the water?) to come from the eyes.

There are four vessels which branch on the head. They distribute themselves in the scalp (neck?), where they nourish and cause to grow the abundance of hair. These form unions (with one another).

If the air enters into the nostrils it is driven into the heart and (goes) through the intestine (by these vessels?), which distribute it to the whole body.

When one hears the passage (of the wind), there are two vessels making it to go into the cavity beneath the eye (antrum?). It is otherwise said that if one hears the passage of it, it is that which is in those (vessels) in the forehead. The wind makes a noise which is heard when one breathes.²

If the heart absorbs water, the limbs become wasted.

If the heart palpitates, it is the vessel named the constrictor which causes it: it carries fluid to the heart. It is otherwise said that it makes it³ to close. If this is audible on account of the opening of its orifice, it affects all parts, the heart being oppressed (confused).

If excitement seize upon the heart, there is a rushing (of blood?) to parts of the intestine and to the liver. The vessels of the ear become filled before that the heart has become quieted.⁴

¹ The writer evidently compiled these notes from different sources, and prefaces extracts from the authorities with the words *ki thed*, "it is otherwise said."

² Intestinal diseases with borborygmi are common in Egypt.

³ This passage is obscure.

⁴ This has probably some reference to the curious belief mentioned in the succeeding paragraph.

There are four vessels to his two ears—two together to the right and two to the left. The breath of life enters into the right ear, and the breath of death into the left ear. It is otherwise said, it (the breath of life) enters into the right ear; the breath of death into the left.

There are six vessels to the two arms—three to the right and three to the left, extending to the fingers.

There are six vessels to the two legs—three to the right leg, three to the left leg, going down to the soles of the feet.

There are two vessels to the testes, which carry semen.

There are two vessels to the kidneys, one to each kidney.

There are four vessels to the liver, to which they bring fluid and air. These give rise to all kinds of disease when they (*i.e.* the fluid and air) are poured into the blood.

There are four vessels to the intestine and to the spleen carrying to them fluid and air.

There are two vessels to the bladder, which carry urine.

There are four vessels which extend to the anus, which supply it with fluid and air. These are over the anus, opening into it, two of these vessels—one on the right and one on the left—come to it from the leg. They cause dryness of the fæces.¹

Here follow twenty-two short sentences, aphorisms, dealing with different diseased conditions affecting the heart. After which, on p. 103, is a second series of anatomical memoranda, said to have been extracted from an old book, which was found beneath the feet of a statue of the god Anubis, in the city of Letopolis, in the time of Hesepti, the fifth king of the 1st Dynasty, who reigned about the year B.C. 3700.

In man there are twelve vessels² from the heart, which go to all members. There are two in him in his body affected in disease of the intestine. [Then follows a prescription for this disease.]

There are two vessels in him to the thighs. If he have pain in his thigh and his two limbs quiver, then say thus concerning it: "It is a vessel which goes to the thigh which has carried the disease." [Then follows a prescription.]

¹ This passage is obscure.

² Although twelve are specified there are twenty referred to in the succeeding paragraphs.

If he has disease in his neck and pain in both eyes, then say thus: "It is the vessels of his neck which have carried the disease." [Then follows a prescription.]

There are two vessels in him to his arm. If he is diseased in his arm and his fingers quiver, say then—"There are dilatations." [Then follows a prescription.]

There are two vessels in him to his scalp; there are two vessels in him to his forehead; there are two vessels in him to his eye; there are two vessels to his eyebrow; there are two vessels in him to his nostril; there are two vessels in him to his right ear, and the breath of life goes through them; there are two vessels to his left ear, and the breath of death goes through them. These all come together from his heart and are distributed to his nose; they pass together to the hinder part. Diseases of the bowels arise on account of their being emptied. They become emptied through the vessels of the thigh from the first until death.

NOTE ON A MODERATOR BAND IN THE LEFT VENTRICLE AND A PERFORATE SEPTUM OVALE IN THE HEART OF A SHEEP. By R. J. M'CLELLAND, Student of Anatomy, University of Edinburgh.

LEFT MODERATOR BAND.

IN vol. xxxii. of the *Journal of Anatomy and Physiology*, Professor Sir William Turner published an article describing a moderator band in the left ventricle of a human heart. In this, the third specimen which he has described, the moderator band of the left ventricle was quite as thick and as muscular as that of the right.

The writer, when dissecting a sheep's heart, noticed a structure that obviously corresponded to that above mentioned. The left ventricle was opened by Sir William Turner's method—an incision made parallel to and immediately to the left of the anterior interventricular groove. Had the ventricle been opened in the usual way, by transfixing, the band would certainly have been destroyed, and its presence would not have been observed.

A muscular structure was then seen to pass across the cavity of the left ventricle in its lower third. It was attached by one end to the septal wall, 21 mm. above the lowest part of the ventricular cavity, and by its other extremity to a point upon the posterior wall somewhat nearer to the apex, and a short distance below the base of the posterior papillary muscle. Its length was 16 mm., and its diameter 1 mm.

A few endocardial threads were seen at different levels in the ventricular cavity. Several of these passed from the septal wall to the anterior papillary muscle, and others connected the two papillary muscles. The moderator band was also associated with two similar threads, one passing from it to the septum, the other from it to the posterior papillary muscle.

The cusps of the mitral valve and the semilunes of the aortic valve were smooth, and showed no trace of endocarditis. The right ventricle contained a well-developed moderator band in the usual position.

PERFORATE SEPTUM OVALE.

Another point of interest in the same heart was the incomplete nature of the septum ovale. There was present a small opening in its anterior and inferior part, which allowed of the passage of an ordinary quill. Looked at from the right auricle, the opening was slit-like in character. When the left auricle was opened the foramen was not seen until a valve-like flap which concealed it was raised. From the margin of this flap filaments of endocardium passed to the anterior wall of the auricle.

Little blood could have passed from right to left auricle, as in the foetal heart, and it seemed as though none could have gone in the opposite way. If, when the auricles contracted, the blood pressure had been greater in the left auricle, the valve-like flap would have shut to, and the endocardial filaments would have prevented it being driven into the foramen, and thus the passage of blood from the left to the right auricle would have been impossible.

EIGHTH REPORT ON RECENT TERATOLOGICAL LITERATURE. By **BERTRAM C. A. WINDLE**, D.Sc., M.D., M.A.,
Professor of Anatomy in Mason University College, Birmingham.

[The author of this report will feel greatly obliged if writers on teratological subjects will supply him with reprints of their papers, for use in the preparation of future reports.]

I. EXPERIMENTAL.

FÉRÉ (i.) tried the experiment of *incubating fowls' eggs* into which small quantities of a 1 p.c. salt solution had been injected. Other eggs, into which similar quantities of sterilised water had been injected, were incubated at the same time for the purposes of comparison. Under normal circumstances no very special difference was perceived between the two classes of eggs; those which had received the salt solution having, however, a slight advantage, as will be seen from the following statement:—Of eggs injected with 0·5 p.c. of fluid, 71·11 p.c. of those with salt solution and 70 p.c. of those with water developed normally. Where 1·0 c.cm. were injected, the percentages were 65·47 and 60·71 respectively. A second series showed a curious difference. The eggs in this case had been laid five days before incubation, and during the intervening period a very severe storm had passed over the part of Paris where they were. In the case of this group of eggs, the difference was considerable between the eggs injected with salt and with plain water. Of those which received 0·5 c.cm. of fluid, the percentages were 70, 83 and 25, and of those which received 1·0 c.cm. 58·35 and 8·33 respectively. The author thinks that if, under normal circumstances, the difference is *nil* between the action of the two fluids upon the nutrition of the embryo, and if a difference manifests itself under special meteorological conditions, one must admit that the quantity of salt is sufficient to neutralise the effect of those conditions. There is no doubt that storms have an effect on incubation, which effect may be due to a fermentation set up in the egg, against which the small quantity of salt may act as a preventative. The same author (ii.) tried the effect of the vapour of chloroform upon fowls' eggs. When exposed to the vapour for a short time, and then given a period of rest before incubation, the percentage of normal developments was 52·08; when the incubation followed immediately upon the exposure to the vapour, the percentage was only 27·08. The percentage in the control eggs was 81·25. After the eggs had been exposed to the vapour for twenty-four hours, there was very rarely any development, even if the eggs had been given a period of rest of equal duration.

Sulphate of atropia and cocaine were found to produce toxic and teratogenic effects upon eggs. A third paper by the same author (iii.) gives the results of his efforts to produce artificial teratomata. This was done by grafting early chick embryos under the skin of fowls. These experiments, which are of great interest in connection with the embryonic rudiment theory of tumours, show that though after a blastoderm has been transplanted it may apparently be absorbed, yet after a latent period so long as to give rise to the idea that it has completely disappeared, a development of tissue which was not differentiated at the time of implantation takes place. Various tissues may be developed from these grafts, which being of forty-eight hours' incubation consist of almost undifferentiated embryonic tissue. Thus epidermal cells have been found encapsulating a tumour which contained striped and smooth muscular fibres, elastic tissue and vessels. These tumours, however, spontaneously disappear, the greater number not persisting more than two months. It is also interesting to note that there is a certain specificity in germs, even at an epoch prior to that at which histological and morphological characters are distinguishable. Thus duck embryos will not develop on a fowl or a pigeon, nor will those of the chick develop on the pigeon or the duck. Embryos introduced into the peritoneal cavity produced no result. The grafts were usually made in the pectoral region, but will take effect elsewhere. Section of nerves and other efforts to avert phagocytosis produced no effects upon the grafts. These took better in adult than in young fowls. Some of these cystic tumours persisted longer than others: one, for example, made from a forty-eight hours embryo in the region of the sternum, was removed at the end of five months, and was then found to consist of fibro-muscular bundles, with blocks of cartilage and osteoblasts. A further series of experiments by the same author (iv.) was carried out with the object of ascertaining how far traumatism of the egg interfere with the development of the embryo, such an observation being an essential preliminary to experiments such as those of Fol and Warynski, in order that the point may be settled as to whether the operation upon the embryo is the sole factor to be considered, or whether that upon the eggshell must not also be taken into account. In the first series of these experiments a portion of the shell was removed, and a sterilised watch-glass cemented over the opening thus formed, with silicate of potash. In spite of every precaution, the survival of the embryo was rare and of short duration. The second series followed Beguelin's method of removing a portion of the shell over the air-chamber, and substituting for it a portion of sterilised shell from another egg. The result here was more successful, but no fully developed embryos were formed. At the end of 48 hours' incubation there were 31 monstrosities out of 155 developments. In the third series the method suggested by Preyer was pursued, the contents of the egg being incubated in a sterilised glass. As pointed out by Preyer, a fair number of these survived for a time. All these facts show that if the resistance of the embryo of the chick to wounds of the shell is much more considerable than is generally

believed, it is not such as to permit the utilisation of these various methods of uncovering the embryo for the artificial production of monstrosities. It is not possible to distinguish the effects which are produced by the opening of the egg from those due to the latter proceedings. Duplicity of the heart and omphalocephaly, which Fol and Warynski thought they had obtained in consequence of a local momentary compression, may be produced by all the influences capable of disturbing the evolution of the embryo, and amongst others by uncovering it. The influence of local injuries can only be determined by the frequent production of unilateral abnormalities. In any case the possibility of the development of an embryo in an uncovered egg during a considerable time is interesting, because it enables us to follow directly the development of certain malformations of the embryo if it be examined at stated intervals. CHIARUGI and BANCHI (v.) find that an *increase of temperature* renders the process of development in the ova of *Salamandrina* more rapid and active. But these ova only tolerate an increase of temperature within very narrow limits. A temperature of 25° to 28° C. only permits of development for a short period, after which the embryos become profoundly altered or perish. A temperature of 20° to 23° permits of a regular development, but renders the eggs more disposed to abnormal evolution. The greater tolerance of cold than heat is in consonance with the period of the year at which the deposition of the ova takes place. CHIARUGI and LIVINI (vi.), experimenting with ova of *Salamandrina perspicillata*, found that absence of light, or, in a less degree, violet light, induce generally a slight but not harmful delay in development, but may under certain conditions produce graver effects. A serious delay in development, with alterations in and even death of the embryo, may follow as a consequence upon the deprivation of the luminous stimulus.

II. GENERAL.

GIACOMINI, in his tenth communication (vii.), describes two typical *nodular embryos* of which in one all the foetal annexes, save the chorion, were absent, whilst they were all present in the other. In the first, traces of tissues representing the embryo could only be made out with the aid of the microscope. In the second, the embryo was reduced to the condition of a small elevation, slightly enlarged at its free end, and implanted on the internal surface of the amnion. No definite embryonic structures could be made out in it by the microscope. In the first case the disturbing cause must have occurred very early—in fact, when only the germinal disk existed. In the second it occurred at a later period, and the effects were limited to the embryo alone. FÉRÉ (viii.) narrates the history of a *family affected with similar malformations*. The father, a man of 48, was healthy, save that he suffered from malarial fever throughout the time that the children were being con-

ceived. The mother was also healthy. The three children, all males, had retarded dentition, began to walk late, had convulsions whilst teething, and the last two did not begin to speak until they were nearly three years old. In each case the lower incisors were remarkably small, the superior dental arch projected considerably in front of the lower, and the chin was small and short. Each was affected with a very similar form of spasmodic tic, which consisted in a simultaneous elevation of the shoulders and flexion of the head. Each boy had also special minor malformations, such as asymmetry of the face, inguinal hernia, and genu valgum. LEWIS (ix.) gives an account of a case of *iniencephalus*, where the monster was one of uniovular twins, its fellow being a normal foetus of $5\frac{1}{2}$ months' gestation. A review of the literature of the subject is appended, together with a description of the dissection of two hitherto unpublished cases which he found in the museum of the Rush Medical College. BALLANTYNE (x.), in his paper entitled *Teratogenesis*, gives an account, with a full bibliography, of the theories of the past as to the causes of monstrosities. It contains a very interesting discussion of the question of maternal impressions, in which the author asks two questions: (1) Does a definite impression upon a pregnant woman's mind often or ever cause a defect in the foetus, closely resembling the thing producing the impression? (2) Has the state of the mother's mind during gestation any effect upon her unborn infant's development? The first of these questions he answers in the negative, and the second in the affirmative. He regards it as impossible, and here, I think, all teratologists will agree with him, for the sight of a mutilated individual to be so transmitted mentally by the mother as to cause a foetal amputation resulting in a similar deformity *in utero*. On the other hand, he thinks that there can be no doubt that prolonged or strongly-marked mental states of the mother may affect the development of the foetus in the uterus. That such can produce abortion, none, he thinks, will deny; and that, short of producing miscarriage, they can also lead, through vascular and nutritive disturbances, to irregularities in embryogenesis, is extremely probable.

III. DUPLICITY.

FÉRE (i.) gives an account of the *development of the embryos in double-yolked eggs*. He has observed twelve of these eggs, each of which was subjected to 72 hours' incubation. (a) In four cases no development took place, and in three of these the two yolks were intimately united to one another; the two cicatriculæ, instead of occupying their normal position when the egg lay horizontally, were displaced about 40° nearer to the small end. In the fourth, the two yolks were free from any connection with one another, and the cicatriculæ occupied their normal position. (b) In six cases, where the two yolks were intimately united for a greater or lesser part of their extent, there were normal or abnormal embryos, whose

position was nearly that of the cicatriculæ in the first mentioned three eggs, there being the same deviation towards the lesser end. In these six eggs there were six normal embryos. Two eggs contained two normal embryos, the smaller in each case on the yolk which was nearest to the larger end. Two eggs contained one normal embryo on the yolk nearer to the smaller end. On the second yolk there was in one case a cyclops, in the other a specimen of omphalocephaly. Two eggs contained only abnormal embryos, the less defective being on the yolks nearer to the smaller extremities: one cyclops with a double heart and one spina bifida. On the second yolks the two embryos were only represented by simple grooves. Besides their abnormal positions, the eggs with united yolks had their embryos lying with various deviations of their axes. In the two which contained normal embryos, that which was nearer to the smaller end was twisted about 45° to the right, the other to the left for about 135° , i.e., the head and back of the first and the tail of the second were turned towards the right of the observer. In the two eggs which contained one normal and one abnormal embryo, the two were deviated by 45° towards one another in one case, and away from one another in the other. A similar disposition was found in the eggs which contained two abnormal embryos. (c) In two eggs the yolks were independent: each had two normal embryos without deviation, and occupying their normal position. In one the two embryos were equal, in the other the embryo which was nearer to the larger end was slightly more developed, and had a more extensive area vasculosa. These facts confirm former observations. When the two yolks are mobile and free from one another, development may be normal on both. When they are adherent, the adhesion occurs in such a manner that one of the cicatriculæ is nearer to the zone of adhesion, and, as a result, there is an obstacle to development, which leads to the production of a monstrosity, or, at least, of an arrest. Usually it is the embryo lying nearer to the small end which is the better developed: this may be explained by remembering that the cicatriculæ occupy the highest positions whilst the egg is passing through the passages; thus it is the germ upon the higher yolk which finds itself the more free when the union of the yolks takes place. TARUFFI (xii.) supplements his paper upon classification, referred to in last year's Report, by the following observations upon *double monsters of asymmetrical form*. Firstly, the author establishes the limits of his subject, then enumerates the forms of asymmetry, and considers which individuals deserve the name of parasites; then he deals with the frequency of these forms with respect to the various parts of the body, in man and in domestic animals. He draws the following conclusions:—(1) Two complete twins, joined either directly (*disomi sineriti*) or by the medium of the cord (*disomi dieriti*), whether symmetrical or the reverse, both originate from two true twins. (2) When the duplicity is complete, asymmetry is produced by (a) all the grades of aplasia in one of the two twins, beginning with microsomia as represented by Licetus in the para-cephalus adherent to the epigastrium of his brother, and descending

through all the varieties of teratoma ; or, again, (*b*) from the absence of one or more parts of one twin, *e.g.*, an ischiopagus without a head (*Ibi-acephalus*, Taruffi). (3) When the duplicity is incomplete and asymmetrical, it may be due to diverse causes:—(*a*) to aplasia of one part, which sometimes seems to be an appendage adherent to the twin, the incomplete portion then being called the parasite, and the other the autosite ; (*b*) to heterotopia, when the parasite is reduced until only a limb remains, which adheres to the autosite in some unhomologous part ; (*c*) to deformity, when one part is doubled or altered in any region, *e.g.*, by hare-lip, cerebral hernia, hydrops, retention of urine, etc. ; (*d*) to a defect of parts, when in one twin the head or head and trunk are wanting and the pelvic limbs alone remain, or the trunk may be wanting, and the head, with a part of the neck, may adhere to the autosite. (4) Twins of the human species may adhere to any portion of the anterior or lateral aspects of the body, but only to the sacral region on the posterior. In mammals they may adhere to any part of the body. (5) Partial duplicity, more or less asymmetrical, of the viscera or limbs, where the theory of two embryos would be absurd, is generally explained by a division of the duplicated part. The author would substitute for this hypothesis—(*a*) an arrest of development, as in uterus didelphus ; (*b*) a post-generative dichotomy by a double gemmation, as in accessory adrenals or polymastia ; (*c*) division, as in the case of a nose divided by amniotic band. (6) There are some cases in which the origin by division or duplicity is doubtful or erroneous, *e.g.*, an accessory cerebral lobe, double heart, accessory limb on the scapula or ilium, double penis, multiple duplicity, external or internal. (7) There are not sufficient data to determine whether symmetrical or asymmetrical duplicity is the more common. (8) The most common form of asymmetrical duplicity in man is the teratoma, which may be found in all regions of the autosite, but especially in three places—the mouth, the abdomen, and the sacrum. In animals, teratomata are rarely found in these positions. (9) The presence of supernumerary limbs attached to the scapula or ilium is much more common in man than in animals. Such limbs are found not only in the vicinity of the normal limbs, but also in other parts of the autosite, constituting those forms of heterotopia known as *Cephalomelia*, *Notomelia*, *Gastromelia*, etc. These forms of parasitism are fairly common amongst calves and lambs. (10) In man and animals are found, with less frequency than teratomata, parasites with no head, or an imperfect one, which adhere to the thorax or abdomen or pelvis of the autosite, analogous to the *acephali* and *paracephali* which are met with amongst the *Acardiaci*. (11) Hitherto few cases have been met with in man of a parasite consisting of a head and neck without limbs or trunk (*Cephalo-pseudo-acormus*) adhering to the head or epigastrium of the autosite. Such cases may resemble the *Cephalo-acormi*, also of very rare occurrence. (12) Duplicity of the bony parts may occur without duplicity of the corresponding external parts. In the face the number of mandibles may be increased with or without an increase in the number of

mouths. This form of duplicity is rare in man, more common in sheep and calves. BERGKAMMER (xiii.) found in the pelvis of a child, which also had a dilatation of the bladder, a true *teratoma* with a connective-tissue capsule. He describes it as a case of *inclusio foetalis*. It lay between the bladder and the rectum in the true pelvis, and was partly solid and partly cystic. MUZIO describes (xiv.) a *teratoma of the hard palate*, about an inch in diameter, which occurred in a new-born child. The principal part of the tumour consisted of adipose tissue, with connective-tissue trabeculae. It possessed large vessels and a small quantity of striped muscular tissue. It was covered with skin, supplied with hair-bulbs, arrectores pilorum, and sweat-glands.

SANGALLI (xv.) narrates a case in which the head and neck of a young fowl were found growing from the left side of the crop of a pullet nine months old. The author regards this case, which is apparently unique, as one of *gastric teratoma*, analogous to an epignathus.

IV. HEAD AND NECK.

v. MONAKOW (xvi.) gives an account of a case of *cyclopia*, in which there were some remarkable facts observed in connection with the nervous system. Both eyeballs were in the same orbit, and were united to one another, and there was a very slight cartilaginous rudiment of a nose. The central nervous system presented the following noteworthy peculiarities:—(a) There was a single hemisphere, with no trace of a longitudinal fissure, and only a few slight cross depressions upon its surface. There was no sign of olfactory tract or bulb, or of corpus striatum. The anterior pillars of the fornix were present with medullated fibres. There was only an indication of an anterior commissure without medullated fibres. (b) The optic thalami were both present and fairly normal, the right being slightly smaller than the left. The ganglion habenulae and the tæniæ were well developed. The development of the nerve cells in different parts of the thalamus was very unequal. The tuber cinereum and corpora mammillaria were present; the cerebral peduncles failed on both sides. Two small optic tracts passed to the middle line, where they united to form a single optic nerve, which on microscopic examination showed a crossing of some of the fibres. (c) The mid-brain was chiefly represented by the lamina quadrigemina, on which the longitudinal groove was tolerably well marked. The transverse was absent. (d) The remainder of the brain showed two abnormal curves, a second basal and a second dorsal, and, as a consequence, a great part of the cervical cord was invaginated in a hernial manner over the met- and epencephalon, between the rudiments of the cerebellum. In spite of this, the later development of the cervical cord, the met- and epencephalon had not been seriously interfered with, but the cord lay between the halves of the cerebellum, and formed the roof of the fourth ventricle. The separated cerebellar hemispheres each possessed one-half of the

medulla oblongata, an interspace existing between the two parts. There was no pons. The dorsal part had in its intracranial portion a longitudinal fissure, which developed in that part of the cord which lay in the spinal canal into two independent cords, each with its own central canal. In the lumbar region the development of the two cords was most marked, each being of much the same size, but further forward the right cord was the smaller, and lay dorsal to the left. (e) All the cranial nerves coming from the medulla were present, and paired. (f) Various tracts of medullated fibres were met with, some highly irregular, but others recognisable. With regard to the origin of the abnormalities, no traces of pathological action were discoverable, and the author thinks the disturbance must have occurred in the first week of life. It is remarkable that the central nervous system should have proceeded so far, and in many ways also so normally in its development, considering the early period at which it was affected, and the disadvantageous conditions under which it had to develop. A further description of the conditions met with in the nervous system of this foetus is given by NÆGELI (xvii.). LEVI (xviii.) describes the *brain in a case of idiocy*, due to arrest of development. The child, a female aged 3, had a very small brain, the weight being only 250 grammes, which is the normal weight at the time of birth. The convolutions were extremely simple, the ascending frontal was connected with the second by an annectant gyrus, and the second, third, and first were connected with one another anteriorly. There were apparently no olfactory bulbs at the end of the tracts. CLAISIE and LEVI (xix.) have examined microscopically the choroid plexuses in a case of *internal hydrocephalus* in a child æt. 3, and compared them with those from normal brains of the same age. The former showed a distinct and well-marked hypertrophy, which the authors think may have been the cause of the hydrocephalus. SAINT-REMY (xx.) describes an embryo which had been accidentally obtained in an over-heated incubator. It showed *torsion of the axis of the body* with anencephalus, and was of the development of the third day, though it had been only 45 hours in the incubator. In the cerebral region the development was normal, except that the medullary plates had not folded over and united, but remained horizontally extended. In the mid-brain, on each side of the external borders of the medullary plate were paired epithelial buds, of which the anterior were the larger. As to the nature of these outgrowths, he points out that observations upon fishes and reptiles show that the development of the epiphysis and paraphysis was originally paired, but that exaggerated growth of one leads to a failure to develop of the other. Here it appears that the want of union of the borders of the medullary groove had restored independence of action to the two borders, and replaced them, in a certain sense, in their primitive condition. This observation, therefore, seems to show that the actual method of development of the epiphysis and paraphysis of birds by means of a single evagination has been preceded by a method of development by paired evaginations analogous to that which has been observed in certain fishes.

COLLINS and ROLSTON (xxi.), as the result of their examination of seven *microphthalmic eyes* with protrusion of the retina through a gap in the choroid and sclerotic, state that the amount of the protrusion may vary from a small knuckle up to two-thirds of the membrane. The site of the protrusion was nearly always at the lower and posterior part of the globe. In some of the cases the vitreous was very imperfectly developed, being replaced by a kind of fibrous tissue, with blood-vessels coursing through it. In one case a plate of hyaline cartilage was found embedded partly in the choroid and partly in the sclerotic. Sometimes the protruded folds of retina formed fluid-containing cysts.

VOSSIUS (xxii.) describes a *microphthalmic eye* removed from a girl æt. 9. The rudimentary lens, which chiefly consisted of a strongly folded capsule, lay in the anterior chamber in front of the iris. It was connected posteriorly with a fibrous string containing the hyaloid artery. In the folds of the capsule were swollen epithelial elements and vessels containing blood-corpuscles. The folds were united to the posterior surface of the cornea and the pupillar border of the iris. The pigmented epithelium was richly supplied with glands. The choroid was atrophic in places in its anterior segment, and was filled with masses of round cells.

V. LEONOWA (xxiii.). The result of this author's observations on cases of *anophthalmia* is to show that the fourth layer of the calcarine cortex is in a high degree related to the integrity of the eye. This observation is of considerable importance from a general embryological and physiological standpoint, since it points to the fact that the elements of the fourth layer (certainly besides other nerve elements which lie scattered in the remaining layers of the occipital cortex, and which are also absent in cases of *anophthalmia*) play a very special part in the function of vision. (*N.B.*—A reference to a former paper by this author of a kindred nature will be found in Report IV., No. xviii.)

DE BORIS calls attention (xxiv.) to the rarity of the coincidence of *hare-lip* with angioma of the lip. He describes a case of his own, and cites another recorded by Lannelongue (*Arch. Gén. de Méd.*, 1883, 1, p. 397). GIVEL (xxv.) describes a *tumour* which he removed from the gum of a new-born infant. It was smooth, tense, elastic, and covered with mucous membrane. It measured 1.5 by 1.0 cm., and might be classified as a granuloma or sarcoma. There had been no recurrence at the end of six years. FÉRÉ (xxvi.) thinks that the *occipital vortex of hair* over the obelion corresponds to the anterior extremity of the dorsal groove, where it forms a sort of anterior dorsal umbilicus, in a manner analogous to the fossa and vortex of hairs often found at the sacro-coccygeal region. The occipital vortex is rarely median, and often presents lateral deviations to an extent of 20 or 30 mm., the deviation being more often to the right. It may be double; and this form, which is possibly hereditary, is frequent in some classes of degenerates. It may be explained by supposing that the closure of the groove has not commenced exactly at its anterior

extremity. The sacro-coccygeal fossa also presents occasional lateral deviations, and may be, though rarely, doubled.

BLANC (xxvii.) has a paper on the *cervical appendages* (pendeloques, breloques) which are met with in the goat and other animals below the parotid. In the goat each of these contains a plate of elastic cartilage identical with that of the pinna: it usually possesses a few small intrinsic muscles and four extrinsic, three pannicular and one deep, the last passing from the summit of the cartilage between the two divisions of the sterno-mastoid, to be finally inserted into the posterior surface of the pharynx. It is innervated by two filaments from the second cervical nerve and by one from the hypoglossal. A microscopic examination of a goat embryo of the sixth week showed no trace of this cartilage, from which the author argues that it is not part of the *primitive* branchial apparatus, but something superadded. In the pig these appendages and an abnormal cervical fistula (*canal de soyon*) are most common in autochthonous races, as they disappear under the care of the breeder. In some cases the former exist only as simple hair-clad tubercles. The canal is a small passage at the lower part of the parotid, 2.0 to 3.0 cm. deep, and blind. Zundel thought that it was an imperfectly closed branchial cleft, but it is not met with in the foetus, or even in very young pigs. The author considers it to be an invagination of the skin, which at a certain point is adherent to the sterno-mastoid. As the fat increases, the adherent portion is gradually drawn in so as to form the blind end of a tube: thus its origin is not referable to the branchial apparatus. In the dog the warts on the face which are so constant represent the appendages. These appendages are, he thinks, derivatives of the branchial system: the singular deep muscle follows the course of the cleft, passing between the thyro-hyal (third) and stylo-hyal (second) arches, and therefore belongs to the second cleft. It is innervated by the hypoglossal. The appendage therefore belongs to the external part of the second cleft, and is the rudiment of a branchial ear, homologous with the pinna. Thus they are identical with the supernumerary auricles of man. Their appearance is, he thinks, purely teratological, but they are highly hereditary. (*Note.*—A full discussion of these appendages, with notices of the literature, will be found in Bland Sutton's work, *Evolution and Disease*, pp. 84 *et seq.*)

V. THORAX.

GUÉNIOT (xxviii.) describes a case of *supernumerary breast* in a man, which was situated a hand's-breadth internal to the posterior border of the axilla, on the posterior surface of the scapula, and not far from its inferior angle. It consisted of a small but distinctly projecting nipple, surrounded by a strongly pigmented areola, about the size of that of the normal male breast, and surmounted by several long hairs.

SCHMIDT (xxix.) has a paper interesting in connection with the subject of *supernumerary mammae*. He states that in human embryos

of about 15 mm. in length, a line of elevated epithelium, 1.0 to 1.5 mm. in breadth, is to be found on the side of the thorax and abdomen, as well as on the shoulder and pelvic girdles, at the boundaries between the trunk and the extremities. This line he calls the milk-streak. Within or along this streak are to be found in the normal positions the anlagen of mammae of a conical or lenticular form. In the region of the same streak appear in longer embryos, of from 26 to 60 mm. in length, epithelial anlagen of various sizes and positions, which must be looked upon as the earliest stages of supernumerary milk-glands. He has found these anlagen in the region of the axilla, on the anterior and lateral walls of the thorax, and in the inguinal region; in fact, in those places where hyperthelia and hypermastia most frequently occur in the adult. The condition of normal hyperthelia in the human embryo disappears in the process of development. (*Note.*—These observations supplement and correct those alluded to in the Report of last year.) HOFFMANN (xxx.) gives an instance of *absence of the sternal part of the right pectoralis major* muscle in a man æt. 47. The clavicular part and the pectoralis minor were well developed. The right upper extremity was somewhat smaller than the left, the fingers were claw-like, and some of the joints were ankylosed. Webs existed between index and medius, medius and annularis, and annularis and minimus, the last being the most extensive. This abnormality, he says, occurs most commonly in the male, and on the right side. (*Note.*—Other cases will be found in former Reports, viz., I., Nos. 16, 17, 18; III., Nos. lv. and lvi.; IV., Nos. xxiii., xxiv.) FLETCHER (xxxi.) describes a *congenital cyst of the anterior mediastinum*, of the size of a bantam's egg. It was loosely connected with the left bronchus, and more firmly with the œsophagus. It contained a glairy milky fluid, and was lined with columnar ciliated epithelium. It contained two layers of unstriped muscular tissue, circular and longitudinal respectively, but no cartilage. BIRMINGHAM (xxxi.) gives the following statement as to *irregularities of the sternum*:—The majority of sterna—viz., 87 p.c.—are asymmetrical, while about 13 p.c. are approximately symmetrical. The most notable irregularity is a depression of the clavicular facet, accompanied by a corresponding diminution of the vertical depth of the sternum on the same side, present on the right side in 50 p.c. of sterna, and on the left side in 37 p.c. The interval between the articular facets for the first and second rib cartilages is usually less on one side than the other, being narrower on the right side in about 44 p.c. and equal in about 28 p.c. of the sterna. In the majority of sterna the symphysis between the manubrium and gladiolus is oblique, sloping downwards on the right side more frequently than on the left. Finally, there is, in about 59 p.c. of sterna, a longitudinal curve traversing the whole bone, the convexity of which is directed a little more frequently to the right than to the left. PFLANZ (xxxii.) describes the history of a case of *dermoid cyst of the anterior mediastinum*, and gives details of twenty-four other cases collected from the literature of the subject, from which he deduces the following facts:—Males were affected in

about equal proportion to females. The cyst usually occupied the upper part of the anterior mediastinum, and extended upwards, or more frequently downwards and to one side, so as to compress the lung. The size varied, but in one-half of the cases it was very considerable. Sometimes only a few cysts were present, at others the tumour consisted of a complicated multilocular cyst. The cyst wall usually resembled ordinary skin. The author considers that the origin of these tumours is to be referred to the thymus, including the third branchial cleft, which would explain the presence of cylindrical and ciliated epithelium. The so-called dermoids of the lung are really only cases of extension.

BARABAN and SCHUHL (xxxiv.) add another to the list of cases of *obliteration of the aortic orifice* (for a further account of which the abstract of a paper by Apert in last year's Report may be consulted). The child in this case lived five days. An impermeable diaphragm was found to occupy the position of the aortic valves. The interventricular septum was imperforate, and the foramen ovale was slightly open. COYON (xxxv.) describes the heart of a child aged 13 months, in which the aorta and pulmonary artery both sprang from the right ventricle. The former was very small, the latter very large. The interventricular septum was very slightly developed, so that the organ might really be regarded as being univentricular. The same author (xxxvi.) gives another case of a *cardiac malformation*. There was transposition of the great arteries, without perforation of the ventricular septum; thus the right heart supplied the greater and the left the lesser circulation. Persistence of the foramen ovale and ductus arteriosus permitted some mixture of the blood. The heart itself must have been supplied with venous blood, for the coronary arteries came off from the aorta. The child lived fourteen months in a cyanosed condition.

VI. ABDOMEN.

CHAMPNEYS and POWER (xxxvii.) give an account of a case in which a complete *septum* of mucous membrane occluded the *duodenum* immediately above the opening of the bile-duct. The portion above the septum was distended into a sac. KOPS (xxxviii.) describes a *congenital tumour* of the size of a marble, and of cartilaginous hardness, situated at the position of the pylorus. It consisted of greatly hypertrophied muscular tissue, the hypertrophy extending even to the muscularis mucosæ. SANGALLI (xxxix.) describes two cases of abnormalities of the *pancreas*,—(a) an accessory lobe projecting from the upper border of the organ; (b) double pancreas, one part lying in front of the other. The two portions were united near the neck of the organ, the two tails both reaching to the spleen. The same paper contains notes on cases of abnormalities of the *testicles*: (a) absence of the left testicle; (b) duplicity of the right testicle in a man. In connection with this case he notes one which he had previously published of duplicity of the left testicle in a child.

STECKMETZ (xl.) records a case of *rudimentary penis*. There was a scrotum with testicles, and in the situation of the penis a wart with a groove on it, but imperforate. (The child passed urine per rectum.) Under the wart-like structure (subcutaneously) there was what appeared to be a rudimentary penis. On operating, this was found to be a normal but imperforate glans. A list of similar cases is given.

CIOFFI (xli.) gives a case of *double penis* co-existing with *atresia ani*. There were two well-formed penes, each with a urethra, corpora cavernosa, glans, and prepuce. Connected with one was a testicle, with the other an empty scrotal pouch. Faeces and urine were passed from both urethral orifices. (*Note*.—Other cases of double penis will be found recorded in Report VI., Nos. xxviii. and xxix.)

KRAUSE (xlii.) describes a case of congenital *prolapsus uteri*, where there was also *spina bifida* and *prolapsus ani*. He states that only four cases of congenital *prolapsus uteri* have been properly described, and notes that *spina bifida* co-existed in all of them. MANISCALCO and TITONE (xliii.) narrate a case of *absence of the vagina and uterus*. The female was aged 45. There was only one kidney, of double the normal size, which lay transversely across the sacral promontory, and was provided with a very large ureter. The vestibule ended in a *cul-de-sac*; not even microscopic examination revealed any trace of uterus or vagina. There were, however, a pair of tubes with fimbriated extremities, which lay attached to the left side of the kidney, and which evidently were the Fallopian tubes. The ovaries were present.

CAVASSE (xliv.) gives the details of a case of *atresia of the inferior vena cava*. Unfortunately only the right side was examined, but that revealed a curious state of affairs. The inferior vena cava terminated below the renal veins in a cone, from which depended a continuation which shortly became an impervious fibrous cord. The spermatic vein opened into the conical termination of the vena cava, and it was by means of this vein that the blood from the lower extremity reached the heart. There was no communication between the vena cava and the right femoral vein save through this enlarged spermatic, with which the femoral was connected by the anastomosis of the pubic veins. The condition is explicable by an arrest of development of the lower part of the right posterior cardinal. It is unfortunate that the limited nature of the examination did not render it possible to ascertain the course of the blood on the left side, but it is probable that it was similar to that on the right.

VII. EXTREMITIES.

MEUNIER (xlv.), a case of *amelia*. The child, which lived two months, had no arms nor legs. Scapulæ and clavicles were present. The right lower limb was represented by a fleshy appendage with two toes provided with nails. It contained five pieces of cartilage, of

which the upper two were atypical; the lower three somewhat resembled phalanges, and were partly ossified. The two glenoid cavities when examined resembled half spheres, each about the size of the head of a foetal humerus. A careful examination was made of the nervous system, to see how it compared with that of a normal child of the same age. On a naked-eye examination of the cord, the cervical and dorsal regions of the amelic foetus appeared to be larger than that of the normal, the reverse being the case in the lumbar region. The following table shows the relative volumes of grey axis:—

	Amelic.	Normal.
Cervical enlargement, 4th root, .	1·6 mm.	1·75 mm.
" " 7th " .	2·19 "	2·30 "
Dorsal cord,	1·60 "	1·29 "
Lumbar enlargement, 4th root, .	2·04 "	2·16 "

Thus there was a slight arrest of development of the grey matter in the enlargements. Microscopic examination showed a very slight difference in the number of motor cells, which were slightly fewer in the amelic foetus, but their other characteristics, situation, dimensions, form, and staining possibilities were absolutely identical.

STRUTHERS (xlvi.), in a paper on *separate acromion process*, inclines to the belief, after a careful examination of the evidence, that these cases are best explained as being instances of fracture, and not of separation of epiphysis. TILANUS (xlviii.) deals with the subject of *Sprengel's deformity* (described in *Arch. f. Chir.*, 1891). It consists in a congenital displacement headwards of the shoulder-blade; and in the four cases in which the original observer met with it, it was in each instance on the left side. Since the first description, other authors have recorded cases, e.g., Wolffheim (*Zts. f. Orthop. Chir.*, 1896), fifteen cases—nine left, six right. Tilanus describes three further cases, all of the left side. He thinks that the condition may possibly be due to an abnormal situation of the child in the uterus. TARUFFI (xlviii.) describes a case of partial *cryptomelia* in a foetus, where there was encephalocele with serious facial defects, and also extensive thoracico-abdominal fissure with protrusion of the liver. The humeral part of the right arm was covered with the skin of the thorax, by which it was bound down to the ribs. The forearm and hand (which had no pollex) projected free. The pollex was also absent on the left hand. JEANNE (lxix.) describes a case of *brachydactyly of the right index finger*, the only abnormality in a male æt. 45. It measured 4 cm. from the head of the metacarpal to the tip, the medius measuring over the same extent 9·5 cm. The metacarpal of the index measured 5·5 cm. and that of the medius 7·0 cm. The atrophy chiefly affected the first phalanx, which was reduced to the condition of a bony ring, 7 mm. thick at its maximum, and perforated at the centre. The second phalanx was 14 mm. long. The ungual phalanx was much less atrophic than the others, and the muscles were all quite normal. RIDLON (l.) gives the following instances of *deformities produced by*

constriction bands:—(a) A child in which the middle finger of the left hand was amputated at the end of the proximal phalanx; the right middle finger was similarly affected; there was a constriction on the right little finger above the root of the nail, a constriction around the left great toe, and finally a constriction around the right ankle, $\frac{3}{8}$ " deep anteriorly and $\frac{7}{8}$ " deep posteriorly and internally. (b) A case of congenital amputation of both legs at the knee, and of the left arm at the elbow. (c) In another child—(1) right hand, a constriction groove round the middle finger; (2) left hand, all the middle finger beyond the distal end of the proximal phalanx was represented only by "a mere thread," which the mother removed; (3) right foot, the distal phalanx of the great toe was amputated, and the distal and adjacent phalanx of the second toe; the third toe had no nail; (4) left foot, the great and second toes were amputated as on the right side. The third toe was much the largest, and had a constriction band surrounding the second phalanx. CRAWFORD (li.) gives a case of *ectrodactyly* in a Hindu child æt. $2\frac{1}{2}$ years. The hands were centrally split up as far as the wrist, between the metacarpal bones. On the right, the pollex and index formed one claw, and the minimus (?) the other; there were only three digits. On the left there were two claws, each consisting of two digits. There was no hereditary influence traceable. CRÉMAZY (lii.) deals in his thesis with the subject of *polydactyly*. He gives a general account of the subject, together with some new cases, of which the following are the most interesting:—(a) A case of trimerous pollex: there were three distinct phalanges, of which the first and second were ankylosed at their articulation. There was also a small supernumerary index included in the same fold of skin as the true index. (Note.—For the literature of trimerous pollex, see former Reports; a paper by the reporter in this *Journal*, vol. xxvi. p. 100; and Bateson, "Materials for the Study of Variation," p. 327.) (b) Triple pollex, the supernumerary members lying on either side of the normal. (c) A second similar case, with a double pollex on the other hand. MOTTA (liii.) has the following observations upon fifty cases of *absence of the tibia* observed in thirty-nine individuals, eleven cases being bilateral. Nineteen were in males, nine in females, and six in fœtuses (sex not specified). The condition was generally accompanied by deformities of other limbs, the femur of the side being usually altered in shape and size. The patella was often absent, also the crucial and semilunar ligaments. The fibula was generally thickened at its extremities. Heredity does not appear to have any connection with this malformation. HAVEN (liv.) describes a case of *congenital dislocation of both knees* in a female. There was no patella to be felt on either side, the legs were hyperextended so that the toes touched the abdomen, and the heads of the tibiæ were dislocated forwards.

POTER (lv.) deals, in a lengthy and valuable thesis, with *congenital malformations of the knee*. He concludes as follows:—*Bony malformations*.—Both parts of the skeleton may be affected. (1) Superior segment—the femur may be absent, its lower extremity may be bifurcated,

or its condyles malformed. (2) Inferior segment—the tibia or femur or both may be absent, or the tibia may be bifurcated. These malformations may, he thinks, be caused by amniotic bands, but in the great majority of cases he believes them to be due to arrests of development, probably produced by an infection. *Malformations of muscular or neuro-muscular origin.*—Extensor group—genu recurvatum is neither a luxation nor an epiphysary separation. It is a hyperextension of the leg on the thigh, due to a contraction of the triceps during foetal life. The epoch at which the triceps is affected is from the third to the fifth month. This affection is relatively frequent. Absence of the patella does not constitute a definite morbid entity. It is a common malformation which is met with when the triceps is affected at the commencement of its evolution. Congenital atrophy is of the same nature. These phenomena are thus connected with one another; arrest of development of the triceps before the third month—absence of the patella; after the third month—atrophy of the patella; contraction of the triceps—genu recurvatum. The patella may be divided into two portions by the isolated action of the vastus internus. The case described as absence of the quadriceps is rather one of progressive atrophy at the muscle. Flexor group—these muscles may be contracted at birth. Generally other groups are affected at the same time. These contractions are the result of some developmental disturbance of the nervous system. *Malformations of ligamentous origin.*—Congenital dislocation of the patella, which may be displaced upwards, inwards, or may penetrate into the joint. But the true luxation is that which takes place outwards: this is also by far the most common, and may exist under one of two forms. (1) Intermittent—luxation only takes place in extreme flexion, at other times the position of the bone is normal. (2) Permanent—the patella remains fixed upon the external condyle. The etiology is very complex, the principal causes being absence or malformation of the external condyle, extreme looseness of the ligaments, and the action of the vastus externus. Congenital genu valgum and varum are very rare as isolated conditions, but are often found associated with other malformations. Their most common cause is an abnormal action of the muscles. Congenital luxations of the knee are rare: when present, they may be permanent or intermittent. They may be forwards, backwards, outwards, or inwards, but the lateral displacements are less common.

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Notices of New Books.

Mammalian Anatomy. PART I.—*The Skeleton of the Cat compared with the Skeleton of Man.* By HORACE JAYNE, M.D., Ph.D., Director of the Wistar Institute of Anatomy and Biology, and Professor of Zoology in the University of Pennsylvania. Philadelphia: J. B. Lippincott Company, 1898.

THIS carefully prepared and elaborate monograph is well arranged, beautifully printed, profusely illustrated, and is evidently the work of one who knows his subject minutely and practically. But one is inclined to doubt that it will serve the purpose for which it is intended, and this from no fault of its own. Most of those who study Anatomy are medical students, and the percentage of those who can afford the time to begin their anatomical course by engaging in a detailed examination of any type but the human, is, unfortunately, small. The number of branches of knowledge which it is necessary for the unfortunate aspirant to a medical degree to take up is great and growing, and teachers of Human Anatomy have to complain that, owing to the competing claims of other laboratories, there is an increased difficulty in getting hold of their students and compelling them to do an adequate amount of practical work in the dissecting-room. It is therefore only the favoured few, to whom time is no object, that can pursue the course which Professor Jayne suggests, and to which he has endeavoured to attract them by his comprehensive book. There is much to be said in favour of this scheme of working up from some more generalised type to the human body; and for those who can adopt it, Professor Jayne's present book and its successors will no doubt be helpful. But they are conceived, and this instalment is brought out, on a scale as large and elaborate as that of the largest text-book of Human Anatomy; and the prospect of beginning one's course by making up 789 pages on the cat's skeleton is not an inviting one for the freshman. This great size and the necessarily high price of the series will, we fear, prove an obstacle to their very extended utility.

The work is carefully done, and is deserving the attention of those engaged in teaching Human Anatomy. The figures are numerous and clear, the digression on the evolution of teeth puts the researches of Cope and Osborne clearly and concisely; and the historical notes on nomenclature, taken in many cases from Hyrtl's *Onomatologia*, are for the most part good.

As Professor Jayne has not tied himself to the international system of nomenclature, it is a pity that he has not, in some respects, adopted the best names available. One wonders why the lateral prominences appended to the lower articular end of the humerus should be called condyles in the cat and epicondyles in man,—*cf.* pp. 553 and 564. Also why perpetuate the misleading and nowhere appropriate name 'anterior intertrochanteric' line for the upper end of the linea spiralis. It never goes to the lesser trochanter in any mammal.

We note that he uses the name epistropheus for the atlas, following Julius Pollux, but it is a pity to confuse the beginner, seeing that by common consent the International Nomenclature Committee have applied it to the axis. As Vesalius says in this connexion:—"hæc nomina procul dubio a veteribus, qui pueros in Anatome exercebant manarunt." The use of 'epistropheus' for the axis, is, however, much older than Heister. Eustachius refers to it under this name more than a century before Heister was born (*Opuscula Anatomica*, Venet. 1563, p. 239). This, however, is only a small matter, and does not interfere with the utility of the book. If the succeeding parts are up to this standard, the series will form a reference work of great value.

A. M.

ASSOCIATION OF AMERICAN ANATOMISTS.

UPON the invitation of Cornell University, the Association met at Ithaca, N.Y., 28th to 30th December 1897. Morning and afternoon sessions were held on each of the three days excepting Wednesday, when all the affiliated societies met in the afternoon with the American Society of Naturalists.

After a brief introductory by the President, Dr Frank Baker, Dr B. G. Wilder read an obituary notice of Dr Harrison Allen, one of the founders and presidents of the Association. The report of the Secretary-Treasurer, Dr Lamb, showed that there were 105 active and 4 honorary members. Dr Allen and Dr Wm. Laurence Dana (of Portland, Me.) had died, and Dr P. J. M'Court, of N.Y. city, had resigned.

The circular and blanks in reference to the anatomical peculiarities of the negro race were ordered to be modified, and copies sent out for report of cases.

The Association adopted the report of the majority of the Committee on Anatomical Nomenclature, and ordered it to be published and distributed as soon as practicable, accompanied by the objections of the minority of the committee, and comments thereon by the secretary of the committee. Of the neural terms recommended, more than 100 were identical with those adopted in 1895 by the Anatomische Gesellschaft.

The following papers were read and discussed: they were illustrated by specimens, photographs, and diagrams.

Dr P. A. FISH, Ithaca, N.Y.:—"A fluid for the retention of the natural colours of anatomical specimens"; and "Mummification of small anatomical specimens."

Dr GEORGE S. HUNTINGTON, New York city:—"Comparative anatomy and embryology as aids to the teaching of human anatomy in the medical course."

Dr WILDER:—"An adult and healthy living cat, lacking the left arm, excepting the scapula, and having the heart apparently at the epigastrium."

Dr WOODS HUTCHINSON, Buffalo, N.Y.:—"Relative diameters of the human thorax."

Dr D. S. LAMB, Washington, D.C. :—"Pre-Columbian syphilis."

Mr CHARLES H. WARD, Rochester, N.Y. :—"A cranio-mandibular index."

Professor HOWARD AYERS, University of Missouri :—"The membrana basilaris, membrana tectoria and nerve endings in the human ear." Read by Dr Hopkins.

Dr WILDER :—"Certain resemblances and peculiarities of the human brain."

Dr B. B. STROUD, Ithaca, N.Y. :—"The ape cerebellum."

Dr FISH :—"The brain of the fur seal, *Callorhinus ursinus*."

Dr HUNTINGTON :—"The eparterial bronchial system of mammalia."

Dr J. A. BLAKE, New York city :—"The relation of the bronchi to the thoracic wall."

Dr THOMAS DWIGHT, Boston, Mass. :—"The distribution of the superior mesenteric artery."

Dr D. W. MONTGOMERY, University of California, San Francisco :—"Sebaceous glands in the mucous membrane of the mouth." Read by Dr Lamb.

Dr STROUD :—"Notes on the appendix."

Professor S. H. GAGE, Ithaca, N.Y. :—"On the relation of the ureters in the cat to the great veins; with variations."

Dr WILDER :—"A number of specimens of either unusual or specially instructive character."

Mr H. A. SURFACE, Fellow in Cornell University :—"Notes on the fish fauna of Cayuga Lake."

The following papers were read by title :—

Professor GEORGE A. DORSEY, Chicago :—"Description of two Koutenay skeletons"; and "Two examples of unusual ossification of the first costal cartilages."

Dr E. R. HODGE, Washington, D.C. :—"Relation of sex to the size of the articular surfaces of the long bones."

Dr J. T. DUNCAN, Toronto, Canada :—"Anus vulvalis."

Dr WOODS HUTCHINSON :—"A skin heart?"

The following officers were elected for the ensuing term :—Dr B. G. Wilder, Ithaca, N.Y., *President*; Dr Geo. A. Piersol, Philadelphia, *First Vice-President*; Dr William Keiller, Galveston, Texas, *Second Vice-President*; Dr D. S. Lamb, Washington, D.C., *Secretary and Treasurer*.

Dr F. J. SHEPHERD, of Montreal, Canada, member of the Executive Committee of the Association, in place of Dr Huntington, term expired.

The following candidates were elected active members of the Association :—

1. FRANK IRVING BROWN, A.M., M.D., of South Portland, Maine, Instructor of Anatomy, Portland School for Medical Instruction.
2. GEORGE AMOS DORSEY, A.B., Ph.D., Acting Curator of Anthropology, Field Columbian Museum, Chicago, Ill.
3. GRANT SHERMAN HOP-

KINS, D.Sc., Asst. Professor of Anatomy, Cornell University. 4. G. CARL HUBER, M.D., Asst. Professor of Histology, University of Michigan. 5. A. T. KERR, M.D., Acting Professor of Anatomy, Medical Department, University of Buffalo. 6. ALFRED KING, A.B., M.D., Demonstrator of Anatomy, Bowdoin College. 7. EDWARD JAMES M'DONOUGH, A.B., M.D., Demonstrator of Histology, Bowdoin College. 8. JOHN ANDERSON SPRINGLE, M.D., C.M., Lecturer on Anatomy, M'Gill University. 9. ROBERT J. TERRY, M.D., Demonstrator of Anatomy, Missouri Medical College, St Louis. 10. Professor ALBERT H. TUTTLE, D.Sc., University of Virginia.

The following eminent Anatomists of the Old World were elected honorary members:—

Dr MATHIAS DUVAL, Paris; Dr CARL GEGENBAUR, Heidelberg; Dr WILHELM HIS, Leipzig; Dr ALBERT VON KÖLLIKER, Würzburg; Dr ALEXANDER MACALISTER, Cambridge; Dr L. RANVIER, Paris.

It is understood that the next meeting will be held in New York city in the Christmas holidays, in conjunction with the Society of Naturalists and other affiliated societies.

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PROCEEDINGS OF THE
ANATOMICAL SOCIETY OF GREAT BRITAIN
AND IRELAND.

JUNE 1897.

THE SUMMER MEETING of the Society was held in Trinity College, Dublin, on June 10th and 11th.

Professor THANE, the President, was in the chair, and fifty-six members and visitors were present.

The minutes of the last meeting were taken as read.

The following new members were elected :—

1. W. S. HAUGHTON, M.B., Demonstrator of Anatomy, Trinity College, Dublin, proposed by D. J. Cunningham, A. F. Dixon, and F. G. Parsons. 2. J. K. JAMIESON, M.B., C.M., Demonstrator of Anatomy, Yorkshire College, Leeds, proposed by T. Wardrop Griffith, J. Symington, and F. G. Parsons. 3. H. GADOW, F.R.S., Lecturer on Vertebrate Morphology, University of Cambridge, proposed by G. D. Thane, A. Keith, and F. G. Parsons. 4. H. ALCOCK, M.B., C.M., Indian Museum, proposed by A. Keith, E. Barclay Smith, and A. Robinson. 5 and 6. W. SMYTH, M.D., and R. J. JOHNSTONE, Demonstrators of Anatomy, Queen's College, Belfast, proposed by D. J. Cunningham, A. F. Dixon, and G. D. Thane. 7. W. TURNBULL, M.B., B.S., Demonstrator of Anatomy, University of Durham, proposed by R. Howden, D. J. Cunningham, and F. G. Parsons.

Dr T. H. BRYCE showed a pair of *Negro femora*, which presented a double analogy to the Trinil femur: (1) in the presence of pathological exostoses; (2) in possessing the three distinctive characters claimed by Dubois for the fossil bone. The convexity of the popliteal surface on the right bone was due to a ridge from which the femoral head of the biceps arose, while on the left bone the origin of that muscle was marked by a prominent crest above and a tuberosity below, and the attachment of the inner head of the gastrocnemius was also marked by a prominent rough eminence.

The popliteal index of the right bone was 86.5, of the left 92.5, a near approach to that of the Trinil femur, which was 96.9, while the rough, uneven popliteal surface of the left bone suggested pathological change, and exostoses were developed at the attachment of the muscles to the bone.

The interest of the specimen lay in the presence of two factors, morphological and pathological,—the convexity being due in the one bone to the origin of the short head of the biceps from the popliteal surface, in the other to deposit of bone at the attachment of the muscle.

The Trinil femur was also affected by a pathological process associated with exostoses, and the left of these bones suggested a possible hypothesis as to the cause of the convexity of the popliteal surface of the fossil femur. The paper is printed *in extenso* on page 76 of the *Journal of Anatomy and Physiology*—Oct. 1897.

Professor W. SPALTEHOLZ showed stereoscopical photographs illustrating the *Distribution of Arteries in the Human Skin*. The photographs were of specimens of skin from various regions of the body, the arteries of which had been injected with coloured gelatin, the pieces of skin being mounted in canada balsam between two sheets of glass.

Professor H. LÉBOUCQ (Ghent) read the following notes on *The Ossification of the Terminal Phalanges of Mammalian Fingers, in relation to Hyperphalangy*.

1. In the development of mammalian fingers, the phalanges are proximo-distally differentiated by a kind of budding. In the greater number of cases that process does not go further than the differentiation of three (or two) segments, and ceases with the first appearance of the endochondral ossification nucleus, and of the perichondral cap of the distal phalanx.

2. The centrum of the endochondral nucleus is not situated at the very extremity of the phalanx. That nucleus is really a diaphysial one; the distal part of the diaphysis, though it ultimately becomes totally atrophied, owing to the extension of the perichondral terminal cap, yet remains visible for a certain time (human foetus, 4th month).

3. The development of the perichondral cap is in relation with the evolution of the special appendicular organs of the fingers (nails, claws, hoofs, etc.). With the defect of the last (cetaceans, sirenians, insectivorous bats: 2nd–5th finger of the hand), the terminal perichondral cap is also absent.

4. The growth of the thus unlimited finger continues, and indeed

(a) In cetaceans the development of distinct segments oversteps by far the typical number in mammals.¹

(b) In sirenians a fourth phalanx has also been found, but not in all cases.

(c) In bats (*Vespertilio murinus*) I found the 4th digit of the

¹ Probably we should consider here also the separate evolution, by slowness of ossification, of the morphologically equivalent epi- and diaphysis (Howes).

wing in a full-grown foetus to consist of four distinct segments. The number of the foetal phalanges is thus—(from the thumb) 2—1—3—4—3.

5. The distal supernumerary phalanges, without any articular cavity, exhibit a great tendency to unite together by complete coalescence of the cartilage and proximo-distal progress of the ossification. I have previously demonstrated that in foetal cetaceans the number of phalanges is greater than in adult ones. In adult *Vespertilio*, also, the distal phalanx of the two last digits is the second, represented by a skeletal rod, proximally bony, distally cartilaginous, without any trace of articulation between the two parts. There are here, therefore, only two phalanges, instead of four and three in foetal specimens.

6. It should be noticed that the Pinnipeds, with rudimentary nails (*Trichechus*, *Otaria*) possess these appendages well developed in the foetal state; and the perichondral cap on the end of the third phalanx also exists. The adaptive elongation of the extremity to the act of swimming does not take place by means of hypersegmentation of the typical skeleton, but by the development of a fibrous (*Trichechus*) or cartilaginous (*Otaria*) bud from the palmar face of the third phalanx.

Professor A. BIRMINGHAM showed models and specimens illustrating the *Topographical Anatomy of certain of the Abdominal Viscera*.

Dr KAESTNER showed some specimens and photographs of malformed chick embryos,—(1) *hydropic*; (2) with *arrested development of the medullary folds*; (3) embryos of the third day, *whose vascular area contains no blood-vessels, but only blood-islands*; (4) *omphalocephalic embryos* (like those described by *Fol*, *Waryaski*, and *Dareste*); (5) with *abnormal clefts*; and (6) *vascular areas without embryo*.

All these malformations were obtained by interrupting the incubation at a certain early period of development for a relatively long time,—*i.e.*, the eggs are brought from the incubator into a room, the temperature of which does not fall under 18° C., and does not exceed 24° C., 7 to 16 days after 6 hours of incubation, 5 to 13 days after 7 to 18 hours of incubation, and 4 to 6 days after 19 to 36 hours of incubation. If the interruption lasts longer the embryo dies, but a shorter interruption does not hurt the embryo. After more than 36 hours of incubation, no malformations are obtained by interrupting the incubation, but the maximum period is much shorter, at the same temperature (of 18° at the minimum), 72 hours at the end of the second day, 48 at the ninth day, and 24 hours up to the termination of the development. If the interruption occurs at a temperature under 18° C., the maximum periods are much shorter for every stage of development.

Prof. Sir WM. TURNER, F.R.S., read a paper by Mr H. J. STILES on *X Ray Photographs of Mercurial Injections of the Arteries of the Limbs and of the Kidneys*. The paper will be found on p. 83 of the *Journal of Anatomy and Physiology*—Oct. 1897.

Dr W. J. OTIS read a paper on *Some Points in the Structure of the Rectum*. See p. 59 of the *Journal of Anatomy and Physiology*—Oct. 1897.

Prof. A. MACALISTER, F.R.S., read a paper on *A Study of Australian Brains*, which will appear in a subsequent number of the *Journal*.

On a New Arrangement of the Right and Left Lobes of the Liver.

By JAMES CANTLIE, M.A., M.B.

The object of this paper is to demonstrate that the gall-bladder occupies a central position in the liver; that on either side of it lie the true right and left lobes of the liver, and that a line from the fundus of the gall-bladder to the exit of the hepatic veins divides the liver into equal portions, as shown by injections, by weighings, by developmental, by pathological, and by clinical observations. In other words, that the present anatomical division into right and left lobes by a line drawn along the longitudinal (the fissure for the obliterated umbilical vein and ductus venosus) fissure is unscientific, and consequently untrue and untenable.

My attention was first drawn to this subject whilst performing a post-mortem upon a Chinese prisoner, who committed suicide by hanging in the jail at Hong Kong. I mention the cause of his death in order to show that he died of no hepatic ailment, but cut short his own life whilst in good health. At the post-mortem the liver presented the following anomalous appearances. The right 'side' (I use the word advisedly in preference to 'lobe') of the liver existed as a mass of fibrous tissue, and looked like, and practically was, a mere appendage to the left side of the organ. This fibrous mass was adherent to the diaphragm immediately above it; from hence, through the diaphragm and lung tissue to a large bronchus near the root of the lung, an extension of the fibrous tissue showed clearly that a liver abscess had occupied the right side of the liver, and that it had burst upwards through the diaphragm and lung into the bronchus. The completeness of the destruction of the right side of the liver was such that nothing was left to show that the liver cells or vessels had ever existed in that area. With the whole of the right side thus occupied, a marked change in the nature of a hypertrophy had developed on the left side. The increase in appearance made the parts seem elephantine almost, and the weight of the liver was but a few ounces below that of the normal liver. Inspection of the organ, however, brought a new feature keenly home to me. The part which struck one most as regards bulk was the 'lobulus spigelii,' which protruded as a thick, blunt mass of liver tissue. And not only this minor lobe, but the lobulus caudatus, from which it sprang, and the lobulus quadratus in front, also showed this enormous hypertrophy. The hypertrophy of the left side joined with the atrophied right side, at a line drawn through the fundus of the gall-bladder to the centre of the inferior vena cava at the back of the liver. On dissection, the vessels,

veins, artery, and duct of the right side were obliterated, and those of the left side were increased in diameter proportionately to the increase of the bulk of tissue which they supplied or drained.

The only explanation of this pathological state was that an abscess had destroyed the right side of the liver, and that the left hypertrophied and supplied its place and function, so that the man was, hepatically, in as good a state as before his right side had been destroyed by the abscess.

In the course of my reading I came across various statements such as the following:—"The immunity of the left lobe of the liver, not alone from cancer, but from abscess, as well as from hydatids, is a pathological phenomenon to me quite inexplicable. No doubt an anatomical or physiological cause for its immunity must exist, but what it actually is I know not."—(*Harley*.) This remark was called forth by a case recorded by the same author, with reference to which he says:—"But little hepatic tissue remained (in the right lobe); yet, notwithstanding this, and the fact that the diseased growths were secondary to a similar morbid degeneration in the sigmoid flexure, the left lobe of the liver, in spite of being enlarged, was free from disease."

The fibrous state of the right lobe in the Chinaman whose case I have cited cannot be called unique, for at the post-mortem in the Middlesex Hospital, on a case of Dr Goodfellow's (also recorded by Dr Harley), it was found that, whilst the right lobe was studded with cancerous nodules, the left lobe was atrophied, and looked like a mere appendage to the right, not exceeding $1\frac{1}{2}$ inches in diameter. Several other cases could be quoted bearing on the same point, but the above will suffice.

In elucidation of this condition, I venture to submit various observations taken from time to time.

Experiment I.

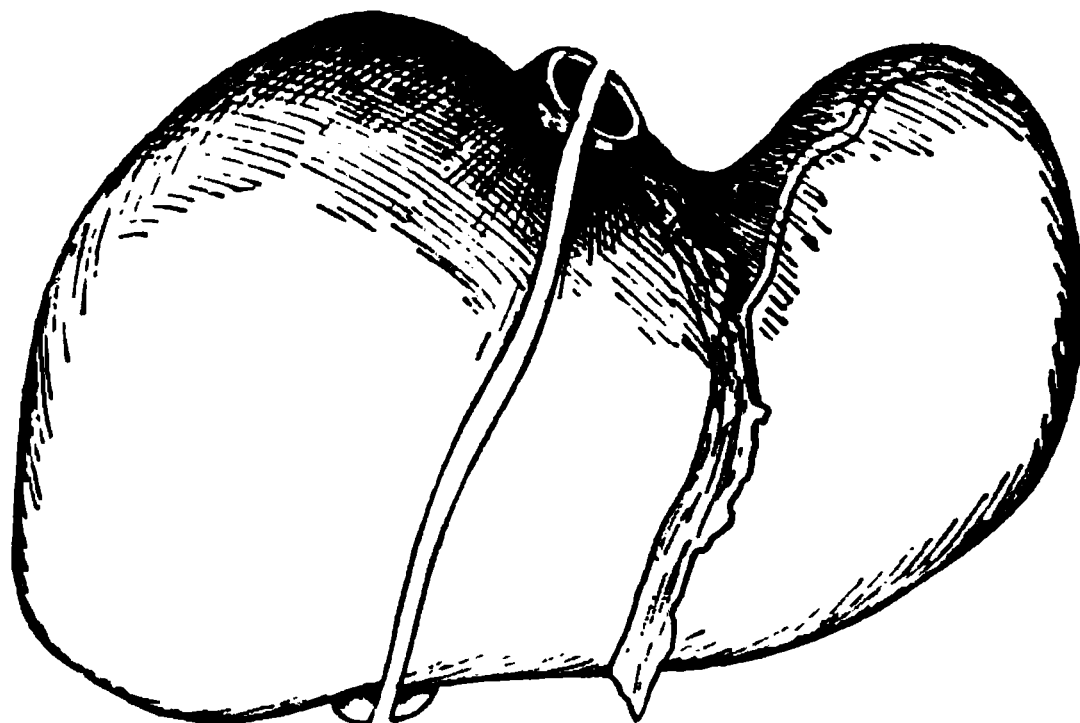
A. The first experiment was merely that of making an incision from before backwards through the liver, from the fundus of the gall-

bladder to the centre of the spot where the inferior vena cava grooves the back of the liver. The weight of the two masses thus divided

approximated each other within a few ounces, sometimes within a drachm or two.

Experiment II.

B. The next investigation led me to examine closely the size of the right and left vessels met with at the portal fissure. The branches of the portal vein could only occasionally be thus gauged, owing to the variability of the seat of its bifurcation; but when the two main



branches parted some little distance before touching the liver substance, the two divisions measured within a few millimetres of each other, that going to the right side being usually the larger.

C. The hepatic artery, by its earlier bifurcation, is more easily dealt with. After the giving off of the branch to the gall-bladder from the right hepatic branch, the diameters of the two vessels approximate each other very closely,—in fact, are almost identical.

D. The hepatic ducts, as they converge to form the ductus communis choledochus, are practically of the same size.

Experiment III.

With this before one, a further investigation led one to injections of the various vessels, and with the following results:—

A. Injections of the right and left divisions of the portal vein, with different coloured substances, showed that the injected areas met along a line, with a wavy outline leading from the centre of the notch corresponding to the gall-bladder, to the notch for the inferior vena cava.

It was not possible to inject the right from the left vessels, nor *vice versa*.

The line where the areas met corresponded to the weight line.

B. Injection of the hepatic artery might, *a priori*, have been expected to afford similar proofs of separation of the right and left sides. The injection does not, of course, yield such patent and easily observed

results as in the case of the vein injections, but it was evident that the left artery usually supplied the accessory lobes to the right of the antero-posterior fissure,—in fact, that at the mid-line the areas injected along the hepatic arteries met.

C. A similar, but not so precise, conclusion was arrived at in the case of the hepatic ducts.

The anatomical evidence seems, therefore, to point to a completely separate vascular supply up to the mid-line of the liver, that line being situated, as above stated, not along the antero-posterior fissure (that

for the ductus venosus and umbilical vein), but along a line drawn from the centre of the notch for the gall-bladder upon the anterior border of the liver, to the notch for the inferior vena cava at the posterior margin.

Clinical Evidence, IV.

Perhaps in malignant disease, more than in any other, is it observed that the disease is confined to one lobe.

A. Dr Pye Smith, in the 31st volume of the *Pathological Society's Transactions*, quotes a case where circumscribed masses of malignant material were limited to the right lobe of the liver.

B. Dr Ewart, in the *British Medical Journal*, September 1860, refers to a case in which the left lobe was free from cancerous material, whilst the right was occupied by a malignant mass weighing 120 ounces.

C. Dr West quotes a case of a child, 8 months old, with a huge hepatic tumour, which turned out to be the almost healthy left lobe pushed out of its place by the diseased right lobe.

Developmental.

The liver is at first an exactly symmetrical organ. The organ arises in the form of two diverticula of hypoblast, which grow from the ventral wall of the duodenum immediately beyond the stomach. The two

diverticula become the right and left hepatic ducts, and the right and left lobes subsequently attain an equal size.

The common bile-duct, although seemingly indicating an asymmetrical development, does not affect the question, as it is formed, not out of a coalescence of the hepatic ducts, but is formed later by a protrusion of that part of the duodenal wall with which the original diverticula are connected.

The apparent asymmetry of the gall-bladder and cystic duct is in the same category, for the lumen of them is formed by a diverticulum from the common bile-duct, itself an asymmetrical tube. And, as in several animals—horse, mouse, etc.—no gall-bladder exists, the consideration of the gall-bladder and its duct may be left out of the question.

It would appear, therefore, that the liver is a symmetrically developed organ from the first; and that it should become asymmetrical afterwards is not in harmony with the development and growth of any other organ in the human body.

Surgically.

The liver, when split or fissured by a blow, as between the buffers of railway-carriages, splits along the mid-line of the liver in preference to any other.

From these considerations, it would seem that the liver is a symmetrical organ in the adult, its symmetry to be gauged not by the antero-posterior or longitudinal fissure (that for the umbilical vein and the ductus venosus), but along a line drawn from before backwards through the fundus of the gall-bladder to the spot where the inferior vena cava grooves the back of the liver. In other words, that we have two lobes (or two livers), which coalesce along a mid-line, giving a right and left half, the left half including the minor lobes, the lobulus quadratus, the lobulus spigelii, and the lobulus caudatus.

In other words, that the gall-bladder occupies a position midway between the lobes, and lies in the groove separating the two original halves. Further, that the inferior vena cava also takes advantage of this interval, and travels upwards between the halves.

The practical bearing of this has yet to be proved surgically; but there can be no doubt that any surgical interference with the liver will be much more readily tolerated as it approaches that line, which I have termed the mid-line of the liver, and that the hæmorrhage has less to be dreaded as the liver is incised or torn in the neighbourhood of that line.

It is theoretically possible to tie the vessels of one side at the gate of the liver, supplying an abnormal growth in one or other of the liver lobes, leaving the other side to do the work.

That one-half of the liver can hypertrophy, so as to perform the function of the whole, is attested by pathological study, in the same way that one kidney can develop so as to carry on the work of the two.

I commend this subject to all those who are working at the surgery

of the liver; and I believe that if, in the hands of future observers, the statements I have made receive closer investigation, the surgery of the liver will be advanced a step.

Prof. R. HOWDEN read a paper on *A Case of marked Distension of the Colon*. It is printed on page 67 of the *Journal of Anatomy and Physiology*—Oct. 1897.

Prof. P. REDFERN read a paper on *The Development and Nutrition of Bone and Cartilage, and on the Relations of Connective Tissues to each other in Health and Disease*. The paper is printed on page 96 of the *Journal of Anatomy and Physiology*—Oct. 1897.

Prof. B. C. WINDLE and Mr F. G. PARSONS read a paper on *Some Points in the Nomenclature of Comparative Myology*. The paper is published on page 522 of the *Journal of Anatomy and Physiology*—July 1897.

Prof. W. ANDERSON read the following communication on *An Undescribed Variation in the Course of the Iliac Portion of the Sigmoid Colon*.

The communication I have the honour to offer to the Society is a small contribution to a steadily increasing list of variations which, though often of little morphological interest, derive considerable importance from their bearings upon surgical pathology and practice.

The typical sigmoid colon may be defined as a coil of large bowel, having the distinctive characters of the rest of the colon, averaging about 18 inches in length, and suspended by a mesentery, except at its two extremities, where it is distinctly fixed to the parietes. This description includes the so-called 'first portion of the rectum.'

The typical sigmoid mesocolon attains a maximum length of about 3 inches near the middle of the coil, gradually diminishing towards the two ends. Its attachment runs downwards along the upper third of the iliac fossa, then curves inwards across the ilio-psoas and the bifurcation of the iliac artery, upwards to the sacral promontory, or even 1 or 2 inches higher, and finally turns downwards mesially as far as the 2nd or 3rd sacral vertebra, where it ceases. So far, the typical conditions. The variations may affect either the length of the mesentery, or the line of parietal attachment of the mesentery (or of the bowel where the mesentery is undeveloped). I propose to speak only of the second of these.

Variations on the line of attachment of the sigmoid mesocolon are probably not very rare. In the past year I have met with two instances in the dissecting-room of St Thomas's Hospital, in which the curve of the iliac attachment, instead of crossing towards the sacral promontory, ran down nearly to the level of Poupart's ligament.

In that now shown (fig. 1) the intestine is seen to run along the whole length of Poupart's ligament, and to be fixed to the iliac fossa

by a mesentery of about $\frac{1}{2}$ inch in length, which opens out and almost completely disappears when the bowel is widely distended. On the under surface of this short mesocolon are three pouches, large enough to admit the tip of the finger, the deepest apparently corresponding to the fossa sigmoidea. The iliac portion of the sigmoid colon has a length of $8\frac{1}{2}$ inches, the pelvic portion lying against the left side of the true pelvis and opposite the great sacro-sciatic foramen, has a mesentery of about 3 inches in length attached to the under margin of the psoas and to the sacral promontory.

*Peritoneum :
Ilio-psoas & os*

Meso Colon

Pelvic Colon

Pubic Crest

or Colon

Iliac Crest

Iliac Colon

upart's Lig



FIG. 1.

FIG. 2.

In the other specimen the arrangement was very similar, but the mesentery was somewhat longer and its attachment higher.

Were a left inguinal hernia to occur in cases of this kind, there would probably be a complete sac containing colon and perhaps omentum; but there is a closely allied abnormality, hitherto seen only in the living subject during surgical operation, which permits a peculiar form of sacless hernia still undescribed in our text-books. Here the intestine, bound to the iliac fossa by a layer of peritoneum covering its front and sides, runs downwards and forwards in the course described (fig. 1) as far as the inguinal region, but the peritoneum is reflected in such a way as to leave an uncovered portion of the gut in contact with the posterior

wall of the inguinal canal (fig. 2). In this case, should the state of the abdominal wall permit a hernia to occur, the protruding portion of colon would be partially or wholly sacless, and the division of the superficial coverings of the tumour would at once expose the muscular wall of the gut, the peritoneum appearing only as a sort of pouch attached to the concave or abdominal aspect of the coil. Such a hernia, if wholly sacless, must almost necessarily be small; but if it be supplemented by a hernia of the pelvic coils of the sigmoid colon, it may assume large dimensions, and present an incomplete sac.

At least six examples of this peculiar form of hernia have been met with; and, by one of those strange sequences so familiar to surgeons, four of these have fallen to my own lot in my practice at St Thomas's Hospital, and all in one year. The particulars of the other two have been related to me by Mr Henry Morris and Mr Leonard Bidwell, who will doubtless publish the details later. The first of my own cases came under my care two years ago¹ when operating for the radical cure of what I supposed to be an ordinary inguinal enterocele in a middle-aged man. The section of the superjacent cutaneous and fascial structures exposed a muscular viscus without any peritoneal investment, and I at first believed it to be a portion of the urinary bladder, but on drawing it further down, it looked distinctly tubular, and a peritoneal pouch was seen to be attached to its upper part. On opening the pouch and introducing the finger, the mysterious protrusion was found to be the colon, and was traced upwards for some distance along the iliac fossa as a sacculated canal, bound down to the iliacus by the peritoneum which passed over its anterior and lateral aspects.

The second and third cases, which followed at close intervals, were of precisely the same character, and both in men. Three months later a fourth case of a more complex kind appeared. A man was admitted with an enormous scrotal hernia on the left side. On operating with a view to radical cure, a peritoneal sac was opened, and within it lay 14 inches of colon. When the gut was nearly reduced, the last 2 inches on the proximal side were found to be covered with peritoneum only on the superior aspect, the membrane being there continuous with that forming the opening of the sac. The bowel on the proximal side could be traced upwards along the iliac fossa, exactly as in the three cases described. Here it was plain that the iliac portion of the sigmoid colon was fixed to the iliac fossa without a mesentery, while the pelvic portion developed a long mesocolon, which was probably attached along the pelvic wall and to the upper part of the sacrum. All four cases recovered without accident, and hence no further examination was possible, but it is unlikely it could have added anything of moment to the observation already made.

All anatomists will agree that such variations should be looked for and recorded, in the interests both of anatomy and surgery; and

¹ *Brit. Med. Jour.*, Aug. 1895.

I venture to suggest that the variations of the sigmoid colon, or of the whole colon, be made one of the subjects of our annual collective investigations.

Dr J. DISSE, Professor of Anatomy at Marburg, read the following notes on the *Early Development of the Olfactory Nerve*.

*Olfactory
Nerve*

Neuroblast

*Olfactory
Cell*

STAGE 3.—Embryo of chick, fifth day of incubation.

It was stated by His some years ago, and corroborated by Kölliker, that in mammals and birds the olfactory nerve arises out of a ganglion. The ganglion cells grow out of the epithelium of the olfactory pit. This outgrowth is preceded by numerous cell divisions on the epithe-

STAGE 1.—Embryo of chick, third day of incubation.

lium, forming round cells, wandering to the outer surface of the epithelium and into the mesoderm, and, being transformed into conical cells, the neuroblasts. The olfactory ganglion consists of these neuroblasts; from the ganglion grow the fibres of the olfactory nerve into the forebrain. Therefore the olfactory nerve is not, as it was believed,

an outgrowth from the brain, but formed by a peripheral ganglion of epiblastic origin.

The ganglion of the olfactory nerve extends from the olfactory pit to the brain. At first it consists only of cells: later, fibres are developed, and it is probable that the fibres proceed from the ganglion cells. Each cell becomes bipolar, and sends out two fibres in opposite directions. Later, the cells are concentrated on the proximal end of the nerve, enveloping the olfactory bulb. At this time the nerve consists mostly of fibres connecting the olfactory bulb with the epithelium of the olfactory pit. The ganglion has been transformed into a nerve.

This statement of His did not describe the ending of the fibres of the olfactory nerve in the epithelium. Some years ago it was admitted that a nervous fibre could be connected with an epithelial cell,—that it could terminate in a cell. On that view were explained

*Ganglion
Cell*

*Olfactory
Nerve*

*Epithelium of
Olfactory Pit*

PLATE 4.—Embryo of chick, fifth day of incubation.

the connections of the nervous fibres with the olfactory cells. Now we are inclined to state that the fibres of the sensory nerves generally have a free termination: if we see a cell connected with a nervous fibre, we take the cell to be a ganglion cell, giving origin to a nerve fibre.

Thus some recent observers regard the olfactory cells ('Riechzellen') of Max Schultze as true ganglion cells, from which the nerve fibres take their origin. This view has been confirmed by the statement of Van Gehuchten, that the fibres of the olfactory nerve terminate freely in the olfactory bulb. Considering the fact that the olfactory fibres are connected with the olfactory cells, and that they have a free termination in the brain, we may be induced to believe that the fibres of the olfactory nerve cannot arise from a ganglion situated at some distance from the epithelium of the olfactory pit. We may expect that the olfactory cells form the ganglion of origin, and in this case

the cells wandering out of the epithelium of the olfactory pit would not have the value of nerve cells.

We may ask, Do the fibres of the olfactory nerve really take origin from the cells situated in the epithelium of the olfactory pit, or do they grow out of a ganglion situated in the mesoderm?

I endeavoured to answer this by means of the method of Golgi. Up to the present I have only succeeded in birds, not in mammals. The best specimens I got from the chick.

The first stage was obtained from an embryo of the third day.

In the epithelium of the olfactory pit there were two kinds of stained cells, different in size and shape. One cell is ovoid, situated near the inner surface of the epithelium, and sending a thin process which passes to the mesoderm. The process ends in the epithelium, near the mesodermic surface. On each side of this cell we find

*Olfactory
Cell*

*Olfactory
Pit*

STAGE 2.—Embryo of chick, fifth day of incubation.

columnar epithelial cells formed at the lower end. The ovoid cell I am inclined to regard as a neuroblast. It is shown by His that such cells are formed early in the epithelium of the olfactory pit.

In the next stage, an embryo of the fifth day, an olfactory nerve was developed, passing from the olfactory pit to the under surface of the forebrain. The fibres of the nerve were only in contact with the thin membranous coat of the brain; they did not enter into the brain itself. The nerve consists of the processes of cells situated in the epithelium of the olfactory groove.

Some of the fibres may be distinctly traced from the origin in the epithelium far into the mesoderm. Each cell sends a long, thin fibre, entering the mesoderm; by convergence of these a nervous bundle is formed, running straight to the brain. Most of these cells show a

second process, directly opposite to the nerve fibre, passing to the inner surface of the epithelium. This process is shorter and thicker than the nervous process; it also appears later.

We may state that the fibres of the olfactory nerve take origin from cells, like the fibres of all the other nerves; that these cells are situated in the epithelium of the olfactory pit, and do not form a part of a ganglion situated in the mesoderm. In the course of the olfactory nerve no ganglion exists; only a few cells are to be seen, of which I will speak later. We may state also that in the first stage neuroblasts are seen, and, later, ganglion cells are developed; so it is very probable that the neuroblasts are transformed into ganglion cells. The neuroblasts do not leave the epithelium of the olfactory pit: they are unipolar cells, and become converted into bipolar cells, resembling the olfactory cells of Max Schultze. Neuroblasts, showing only one long nervous process, are found together with bipolar cells in the same section.

As the specimens, stained after the method of Golgi, show that the olfactory nerve, from the beginning of its existence, consists of fibres, and allow us distinctly to see the cells sending out the fibres, it is easily understood that the cells connecting at this period the epithelium of the olfactory pit with the forebrain have not the value of nervous cells. These cells growing out of the epithelium are very numerous, and cover the fibres of the olfactory nerve, so that they become quite invisible. In the early stages the olfactory nerve only is shown by the method of Golgi.

It has already been mentioned that we find, in the course of the nerve, some cells. These are really ganglion cells, sending out nervous fibres, which are stained by the Golgi method. The cells are found close to the epithelium of the olfactory pit; also close to the brain; they are few in number, though it may be that only a part of them is stained. From the 5th to the 8th day we see unipolar, pyriform-shaped cells, sending out only one fibre, and also bipolar cells. The processes become nervous fibres: in the unipolar cells the fibre is directed towards the brain; in the bipolar cells one fibre is directed to the brain, the other to the olfactory pit. I am inclined to suppose that the proximal nervous process directed to the brain appears first, the distal fibre passing to the olfactory pit being formed later. All the unipolar cells would be converted into bipolar cells. Though I could not find any of these cells showing the two processes for a long distance, I saw some cells possessing a long proximal fibre, and others presenting the distal fibre clearly. It was stated that none of the distal fibres enter the epithelium of the olfactory pit, but there are seen in the epithelium nervous fibres coming out of the olfactory nerve and terminating free on the inner surface of the epithelium, with a small knob. As in the specimens of that stage only the olfactory nerve is visible, and no trace of the fifth nerve is seen, I am induced to adopt the view that the free terminating fibres belong to the olfactory nerve, and that they take origin from ganglion cells situated in the course of the nerve.

It is probable that these ganglion cells are developed from neuroblasts leaving the epithelium of the olfactory pit. His has observed that in the human embryo neuroblasts are wandering into the mesoderm. I can confirm this observation : it is apparently the beginning of the formation of a ganglion, the ganglion remaining incomplete, because most of the nerve cells remain in the epithelium.

In the olfactory nerve of *Petromyzon*, bipolar ganglion cells were seen by Dr Pogojeff (*Archiv für Mikroskopische Anatomie*, Bd. 31, 1888). The same relations exist as in the embryo of the bird. In the olfactory nerve of mammals I have not yet been able to find nerve cells, and I cannot say if these cells in birds are persistent or transitory. Further research is required.

The epithelial cells found in the course of the developing olfactory nerve are destined to form a sheath for the fibres of the olfactory nerve. This sheath was known long ago ; its cells were regarded as belonging to the mesoderm. But it has been shown that, together with the fibres of the olfactory nerve, cells leave the epithelial layer and follow the course of the nerve. They become converted into thin cells, forming sheaths for the nervous bundles.

It is not my intention to enter into a discussion on the morphology of the olfactory nerve. I can only believe that it belongs to the branchial system of the nerves of the head. While of the ganglion cells of the succeeding nerves only one part is derived from the epithelium, in the olfactory nerve all the nerve cells are directly produced by the ectoderm.

From its first appearance the olfactory nerve consists of fibres like the other cranial or spinal nerves. The cells giving origin to the fibres remain in the epithelium of the olfactory pit, where they are situated at the beginning of the formation of the nerve.

In the general and typical relations the olfactory nerve of the youngest embryo is quite similar to the olfactory nerve of the grown-up animals.

Prof. W. SPALTEHOLZ (Leipzig) read the following notes on *Reticulated Tissue : its Relation to the Cells, and its Arrangement in different Organs*.

The connective tissue presents a great many problems of interest which cannot be solved by ordinary methods. One of these interesting points is presented by the so-called reticulated-lymphoid or adenoid tissue, when we study the relation of its fibres to the cells, and also its arrangement in different organs.

Investigations as to these points have been conducted during the past year by myself, and also by Dr Hoehl and Dr Rühle, who have worked under my direction.

So far, we have examined fully-formed tissues only, and have not yet examined them in their early stages of development.

The following is a short account of our methods and results. The first point we inquired into was the relation of the reticulated fibres to the cells. There are two different opinions as to this relation.

According to some observers, all fibres are regarded as processes of cells, while others maintain that an independent system of fibres exists in the form of a network, to which the cells are merely attached or applied.

The difficulty in deciding this point is owing to the fact that in a great measure the network is concealed by the cells, and all methods by which the cells are brushed away may be suspected of producing artificial appearances.

We must therefore find a method by which it is possible to render both parts distinct by colouring the untouched tissue. We succeeded best in the lymphatic glands by using a modified picro-fuchsin colouring (after Van Giesen). By this the fibres are coloured red, and the protoplasm of the cells yellow.

From such preparations (which I hope to have an opportunity of demonstrating to you) it is evident that there exist fibres in the mature organs which are not the processes of cells, but which at certain points—for example, in the sinuses of lymphatic glands—are nearly completely surrounded by the protoplasm of the cells which are attached to them.

In other places, *e.g.*, the liver, kidneys, and intestines, these surrounding cells and sheets of protoplasm are wanting, the fibres being quite naked. I must admit that in many organs, especially during their development, a network of fibres exists, which is formed by the processes of cells, in addition to the independent network which I have mentioned.

By comparing these coloured preparations with others which have been made, either by careful maceration in alcohol and water, 1–3, and shaking, or by digesting with an alkaline solution of trypsin, they do not show anything which is not to be made out by the picro-fuchsin coloration of untouched specimens. The only difference is that the network and its arrangement is much clearer in digested preparations than in others.

The digesting method does not (as many people think) produce artificial appearances, but it must be looked upon as of great value, and, for the investigation of connective tissue, has a superiority over other methods, as it gives great clearness to the arrangement, and can easily be carried out.

During all our investigations we used well-stained material, and at first we digested large pieces in bulk, but afterwards single sections, after having first fixed them on slides. This last method has the advantage that in sections of the same paraffin blocks different methods can be employed; one section can be coloured untouched, the next can be digested, etc.

We fixed the sections on slides which had been absolutely cleaned with distilled water, then freeing them of any trace of fat by steeping in benzin twenty-four hours to seventy-two hours, and then digesting them for twelve to twenty-four hours in an alkaline solution of pancreatin (Parke, Davis & Co., Detroit), then colouring them with iron hæmatoxylin.

I would, lastly, mention that the digestion by trypsin brings out not only the reticulated but also the collagenous fibres: a clear differentiation of these tissues is not yet possible by any means. In deciding whether a fibre belongs to the collagenous or reticulated tissue, we can only conclude from their thickness and arrangement.

Prof. A. FRANCIS DIXON exhibited a number of lantern slides illustrating the mode of *development of the 4th nerve* in the rat embryo. Of interest is the presence of a large number of cells in the course of the intermediate part of the nerve. At certain stages the proximal and distal parts of the nerve are quite fibrous, and resemble in their structure the 3rd nerve, while the intermediate part of the nerve contains very large numbers of nuclei in its course, and resembles a cord of cells rather than a fibrous nerve. The origin of these cells is not from the trigeminal complex, and thus they differ from the cells having a somewhat similar position, which have been described for elasmobranch embryos, by Dohrn, Froriep, and Miss Plat.

Since the fibrous proximal part of the nerve is present before the cord of cells is evident, these cells can in no way represent cells of a posterior nerve root. This cellular structure, in the course of the 4th nerve, is not found in the early human embryo.

Prof. D. J. CUNNINGHAM, F.R.S., read a paper on *The Development of the Fissure of Rolando and of the Calcarine Fissure*. It is printed on p. 586 of the *Journal of Anatomy and Physiology*—July 1897.

A paper on *The finer Ramifications of the Nerves in the Muscles* was read by Dr FROHSE, Berlin. The paper contained the combined observations of Prof. K. v. Bardeleben and Dr Frohse, both having been working at the subject, unknown to each other, for over a year, and both having arrived at practically similar results. Their results showed that there were many nerves ending in the coats and sheaths of vessels, in tendons, in the capsular ligaments of joints and in bones, of such a considerable size that it was a matter of surprise how they could have so long escaped observation. Prof. K. von Bardeleben, who had, in the spring of this year, made a communication on this subject at the meeting at Ghent, was unfortunately unable to attend the meeting at Dublin, owing to illness. Dr Frohse had numerous specimens and drawings of his own to show to the meeting, to demonstrate the points dealt with in the paper.

In 1879 Professor Schwalbe, in his research "*Das Gesetz des Muskelnerveintritts*," came to the conclusion that the point of entrance of a nerve into a muscle or into a muscle bundle (*primitiver muskel*) corresponds to the middle point, or centre of gravity, of that muscle or bundle, so that when a nerve enters a muscle or muscle bundle by a number of branches arranged in a line, the upper and the lower ends of that line are equally distant from the upper and lower ends of the whole muscle, or of the muscle bundle. This observation is some-

what sweeping, and would require qualification for individual muscles as well as for animals of different kinds.

Prof. Hasse of Breslau had published an atlas giving the points of stimulation for all the muscles of the human body, but the drawings are not very clear, and some of the points given are not quite right. The points and lines for the stimulation of muscles which surgeons had arrived at experimentally are more correct. The point of entrance of a nerve within a muscle is not confined to any one small area: there are numerous points, great and small, where the twigs of the nerve trunk enter the muscle. The twigs are distributed throughout the muscle from the tendon of origin to the tendon of insertion, and form numerous anastomoses with each other within the muscle.

It is important to observe that twigs perforate the muscle and end on its superficial aspect, where they become easily accessible to electrical stimulation. The nerves to the tendons coming out of the extra muscular network have especially this tendency to a superficial distribution. Is it not possible that the twigs that terminate on the surfaces of tendons may be the points at which the whole nervous network of a muscle is directly stimulated in the phenomena of tendon reflexes?

The conclusions which had been reached might be thus summed up:—

(1) The point of entrance and manner of distribution of a nerve within a muscle had no correspondence to the shape of the muscle. The form in which nerves ramified varied widely.

(2) Each nerve divides into two branches, or, in other words, the nerve trunk sends off but one branch.

(3) Each nerve, just before entering the muscle, or during its course, rarely towards its termination, gives off one or several vasomotor branches. The exact origin in the central nervous system of the vasomotor twig requires further investigation.

(4) The nerve may enter the muscle along with the vessels, forming a sort of hilus, or it may enter separately.

(5) As soon as the nerve reaches the muscle, it gives off a recurrent branch to the proximal end of the muscle; the more distal the point of entrance, the more numerous and greater the recurrent branches.

(6) The point of entrance—or points, to speak more correctly, for there are commonly several points—are situated,

A. (a) On the deep aspect of the muscle—*facies profunda*;

(b) On the margin of the muscle;

(c) On the superficial aspect of the muscle.

B. (a) Quite at the proximal end, an uncommon situation seen in the *M. semitendinosus*;

(b) Proximal to the point of junction of the upper and middle thirds—common;

(c) At the middle or geometrical middle point—rare;

(d) In the distal third of the muscle—rare.

(7) What is the 'point of entrance'? (*Eintrittsstelle*). Is it the point at which a nerve disappears in a muscle which has not been

prepared by maceration, forceps, and scalpel? No! The 'entrance point' must be regarded, until better can be shown, as the final terminations of nerve twigs visible to the naked eye, twigs of about 0.03 mm. in diameter, terminating in muscle-bundles measuring in breadth about 1 mm. For all such muscle bundles (*primitive Muskeln*, Schwalbe) separate entrance points for nerves are recognisable.

(8) The manner of ramification.—The number of 'extra-muscular' twigs, using the term in the sense defined, is exceedingly great, and there are, of course, a correspondingly great number of points of entrance.

The forms in which nerves ramify are—

- (a) In a preponderating number of descending branches ;
- (b) In long descending, short ascending branches ;
- (c) In nearly an equal number of long ascending and descending branches ;
- (d) In the figure of a '*Fächer*,' the nerve dividing into two branches, there being no central stem ;
- (e) In the form of a *Kegelmantel* (with the same qualification as in d) ;
- (f) In an arborescent form, as in the *Pronator quadratus*, *Anconeus quartus*. The twig may give off branches from one side only, as in the *Psoas major* and *Iliacus*, or from both sides, as in the *Deltoides*.

(9) In the course of muscle nerves numerous extra- and intra-muscular communications take place in the form of loops, plexuses, and anastomoses ; and further, which is a fact quite new as regards higher mammals, there is an INTRA-MUSCULAR PLEXUS. Such plexuses have been found in every one of the larger muscles investigated—*Deltoides*, *Biceps brachii*, *Brachialis internus*, *Supinator longus* (*Brachio-radialis*), the muscles of the forearm, the *Adductor longus*, *Sartorius*, *Gracilis*, etc.

10. The double nerve-supply of such muscles as the *Flexor digitorum profundus*, *Pectineus*, and *Adductor magnus* was observed and confirmed as constant. The *Brachialis internus* (*anticus*) always receives one or more twigs from the *N. radialis* (musculo-spiral). Professor K. v. Bardeleben observed that the *Flexor digitorum sublimis* in many mammals receives twigs from the *N. ulnaris*, and was able to make a similar observation in a human forearm. The branch of the anterior thoracic nerve, which Luschka has described as ending in the deltoid muscle, had never been seen by the authors to end so. This twig, so far as their observation had gone, accompanied vessels, and ended in the tendon of the *Pectoralis major*. The nerve supply of the muscles of the thumb had also been a subject of observation. The anastomosis between the cutaneous branches of the median and ulnar is well known. A communication between the muscular parts of these two nerves has been seen by Flemming. In one hand Dr Frohse had seen this communication very large, in two other hands it was small, and in a fourth hand the communicating branch did not perforate the *Adductor pollicis*, but the third lumbrical muscle. This point de-

served to be emphasised, because in a case where there was section of the median nerve and atrophy of the thenar eminence, reaction could still be got in the thumb muscles by stimulation of the ulnar nerve.

Every one of the dissections which Dr Frohse showed, and which he himself had prepared, showed something new. There is a considerable amount of individual variation in the distribution of a nerve to the same muscle, but the general type of ramification was constant. How far the plexus arrangement of nerves in muscles will affect current physiological problems, whether or not there are ganglionic collections of nerve cells in those plexuses that might act as peripheral regulating centres, or what the exact function of the twigs distributed to blood-vessels may be, are questions which as yet cannot be definitely answered. Dr Frohse has prepared numerous drawings of the termination of nerves in muscles, which are to be published in the *Handbuch der Anatomie des Menschen* (V. Bardeleben), in the part dealing with the muscles and nerves of the extremities.

Dr C. J. PATTEN exhibited the *lower jaw* of an old subject, in which the angle became so widened out that the body and ascending ramus lay almost in one line. With this extreme modification, the neck became very elongated,—a condition probably due to the head of the jaw not obtaining proper apposition with the glenoid cavity. The sockets of the teeth were visible as far back as the first bicuspid, which fact suggests that the absorption of all the alveolar process was not complete, and that the individual to whom the mandible belonged was not exceptionally old when he died.

Dr Patten also exhibited a *cervical vertebra* in which the laminae had not fused; this he regarded as a very rare condition in the lower cervical vertebræ.

Professor D. J. CUNNINGHAM exhibited two models illustrating the *position and form of the kidneys*. One was taken from a dissection of a subject that had been hardened by repeated injections of Müller's fluid for a period of six months. It gave a view of the kidneys from behind, and exhibited their relations to the vertebral column, the twelfth pair of ribs, the internal arcuate ligaments, the muscles of the region, the pleural sacs, the liver, spleen, etc.

The other model showed the kidneys, duodenum, pancreas, and spleen, as exposed from the first in a subject hardened by formalin injections. Professor Cunningham explained that he had prepared this model because the left kidney exhibited in a very perfect way the form produced by gastric pressure, conveyed to it from above, and intestinal counter-pressure from below.

Dr G. ELLIOT SMITH read a paper on the *Morphology of the Fornix and Margin of the Cerebral Cortex*. The paper will be found on p. 23 of the *Journal of Anatomy and Physiology*—Oct. 1897.

Dr WALTER SMYTH showed a living boy in whom the *sterno-costal portion of the pectoralis major*, as well as the *pectoralis minor*, was

absent on the right side. The clavicular part of the muscle was well developed, and the boy was as strong on the right side as on the left. He was right-handed.

Dr C. DE BRUYNE read a paper on *L'adaptation Fonctionnelle de la Phagocytose*. A translation of this will be found on p. 92 of the *Journal of Anatomy and Physiology*—Oct. 1897.

Prof. W. WALDEYER read a paper on *The Topographical Anatomy of the Outer Wall of the Pelvic Cavity, with special reference to the position of the Ovary*. This paper is printed on p. 1 of the *Journal of Anatomy and Physiology*—Oct. 1897.

W. BOOTH PEARSALL, F.R.C.S.I., contributed a paper on the *Linear Determination of the Human Tooth Form*. He showed how difficult it is to arrive at any definite description of a normal set of teeth, owing to the different points of view from which various observers have described teeth. He advocated a diagrammatic method of description, in which each tooth should be treated as a cube, and drawn from six constant points of view, namely, in the upper set, mesial, buccal, distal, palatine (upper), or lingual (lower), crown, and neck. He illustrated his contention by a reference to the unsatisfactory nature of the figures of the tooth of *Pithecanthropus erectus*.

Prof. B. C. WINDLE showed specimens of Priestly Smith's new method of *mounting ophthalmic specimens*. This process has been described in the *Ophthalmic Review* for January 1897.

Prof. R. HOWDEN showed a case of *Bifid Scrotum*. He said that the subject in which the following conditions were found was that of an adult, and was dissected in the University of Durham College of Medicine, Newcastle-upon-Tyne, during the winter session 1896-97.

The penis was $2\frac{1}{2}$ inches (6.4 cm.) in length, and the glans and prepuce were well formed. At the junction of the penis with the perinæum there was seen a small depressed opening, and running backwards from this an elongated fissure 2 inches (5 cm.) in length. At the posterior part of this fissure another opening was seen, and this proved to be the external orifice of the portion of the urethra intervening between the fissure and the neck of the bladder. The fissure was bounded laterally by cutaneous folds, which merged behind it, and which became lost anteriorly on the under surface of the penis. The scrotum was completely bifid.

A No. 6 catheter was passed into the meatus. This traversed the length of the penis, appeared at the perinæal orifice, and remained in view along the whole length of the fissure. At the posterior part of the fissure it again disappeared, and passed along the remainder of the canal into the bladder. The portion of the urethra which extended from the neck of the bladder to the perinæal fissure was subsequently found to admit freely a No. 12 catheter.

On making a dissection of the region, the following conditions were

found :—Each scrotal bag contained a testicle, which, although somewhat smaller than usual, was perfectly formed. The transversus perinæi and erectores penis muscles were well developed, and the crura of the penis were of an average size. The accelerator urinæ muscle consisted of two parts, one on each side of the fissure already described. These two parts came into contact behind the fissure, while anteriorly the muscle was lost on the under surface of the penis. The spermatic cords were normal, and the prostate gland, vasa deferentia, and vesiculæ seminales were all present. On incising each vas at the base of the bladder, a probe was easily passed along the duct into that portion of the urethra which connected the bladder with the exterior.

PHOTOGRAPH OF A CAST OF THE PERINÆUM.

A, penis; *SS*¹, right and left scrotal bags; *O*, placed immediately to the left of the opening of the urethra on to the surface where the penis joins the perinæum; *FF*, folds bounding laterally that portion of the urethra which presented the form of a groove; *An*, anus.

The malformation may, I think, be explained by a reference to the development of the external genitals. (1) The labio-scrotal or outer genital folds have failed to unite in the median line to form a single scrotal bag. (2) The lips of the urogenital sinus have apparently completely united anteriorly to form the urethral canal, while posteriorly they have failed to join, so that here the urethra assumes the form of a groove, bounded laterally by the cutaneous folds already described,—folds which present a remarkable resemblance to the labia minora.

For the facts elicited by the dissection of the region, Dr Howden is indebted to his assistant, Dr William Turnbull.

Mr W. S. HAUGHTON showed a number of *Skiagraphs* which he had taken, illustrating the application of the process in two departments of anatomical investigation—

1st. Ossification.

2nd. Arterial anastomosis.

Illustrating the process as applied to ossification, Mr Haughton showed skiagraphs of the hand, wrist, elbow, foot, ankle, knee, and hip joints, taken at the following ages—foetus 'at term'; 3, 5, 6, 7, 13, 16, and 18 years; and also in young adults.

These represented the skiagraphical appearance of the various centres of ossification at the above ages, and also the dates of union of certain epiphyses to their diaphyses.

A skiagraph of an entire foetus showed well the appearance of the ossific centres 'at term,' and also the enamel in the young teeth, and the semicircular canals in the petrous portion of the temporal bone.

Skiagraphs of abnormalities of the bones of the hand were also shown.

With regard to the skiagraphs of arteries which Mr Haughton exhibited, he stated that, while working at the application of X rays in surgical anatomy for the location of foreign bodies, such as brass pins, coins, etc., in the larynx, trachea, and oesophagus, he found that the ordinary paint injection in the anatomical department gave very good shadows of the arteries and their anastomoses.

An attempt was therefore made to obtain a shadow picture of the arteries in the root of the neck and limbs, merely using the ordinary dissecting-room injection, with a larger proportion of 'red' and 'white' lead introduced.

Skiagraphs taken by this method were exhibited, showing the arteries of the root of the neck, arm, and leg, in which most of the arteries can be recognised, and some of their anastomoses demonstrated.

Both the skiagraphs were taken in the same subject, and the injection had failed to flow in parts of the hand. This is accounted for by the fact that the injection was rather thicker than usual, owing to the increased proportion of 'red' and 'white' lead used; and the difficulty could, of course, be overcome by making a special injection of the main artery of each limb under observation.

Considerable distortion of the relative positions of certain vessels, of course, exists, because the shadows are thrown by vessels lying in different planes; hence the process must not be taken to represent, in all cases, the relations of the arteries.

The advantages claimed for this process are—

1st. That the method of injection (the ordinary dissecting-room method) is *simple*.

2nd. That it seems to promise good results.

3rd. That no special apparatus is required other than that in daily use in every anatomical department.

4th. That no special precautions are necessary in its manipulation.

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PROCEEDINGS OF THE
ANATOMICAL SOCIETY OF GREAT BRITAIN
AND IRELAND.

NOVEMBER 1897.

THE Annual General Meeting was held at Charing Cross Hospital Medical School, on November 26th, 1897, at 4 P.M. Present—Professor THANE (President) in the chair, twenty-three members, and thirty-eight visitors.

The minutes of the last meeting were read and confirmed.

The Treasurer's Report, showing a balance of £80, 10s. 3d., was received and adopted.

In presenting his Annual Report, the HON. TREASURER remarked that the ordinary expenditure exceeded that of any previous year by the sum of £12, as the result of the Summer Meeting. The full cost of that had not yet been met, but looking back upon the success of it, and upon what he ventured to regard as the record number of the *Journal of Anatomy and Physiology* which it had produced, he thought the Society was to be congratulated upon the costliness of the undertaking. He then commented upon the irregularity of receipt of subscriptions during the past two years. He pointed out that the number of members upon the roll exceeded 140, whence it followed that the annual subscriptions, if paid regularly, should suffice for the maintenance of the ordinary year's work of the future, and remarked that, in anticipation of the more regular receipt of subscriptions, he proposed to invest the greater part of the balance in hand as the nucleus of a deposit account. To do so would be to furnish the opportunity of instituting a composition fee, for which some members had expressed a desire, the consideration of which was already before the Committee of Management.

The following gentlemen were elected officers for the ensuing year:—*President*—A. Macalister, M.D., F.R.S. *Vice-Presidents*—A. Birmingham, M.D.; C. B. Lockwood; A. H. Young, M.B. *Treasurer*—G. B. Howes, F.R.S. *Secretaries*—F. G. Parsons (England); J. Musgrove, M.D. (Scotland); W. S. Haughton, M.B. (Ireland). *Council*—T. Bryce, M.D.; D. J. Cunningham, M.D., F.R.S.; A. F. Dixon, M.B.; E. Fawcett, M.B.; Percy Flemming, M.D.; H. Gadow, F.R.S.; Robert Howden, M.B.; A. W. Hughes, M.D.; Arthur Keith, M.D.; J. Yule Mackay, M.D.; G. H. Makins; T. H. Openshaw, M.B., M.S.; A. M. Paterson, M.D.; Arthur Robinson, M.D.; E. Barclay-Smith, M.D.; G. D. Thane; Arthur Thomson, M.B.; G. R. Turner; Sir Wm. Turner, F.R.S.; Bertram Windle, M.D.

Professor MACALISTER then took the chair, and thanked the meeting for electing him.

A vote of thanks to Professor Thane was proposed, seconded, and carried by acclamation.

The following candidates were elected members:—W. H. GASKELL, M.D., F.R.S., University Lecturer in Advanced Physiology, Cambridge, proposed by A. Macalister, E. Barclay Smith, G. D. Thane. R. TRAVERS SMITH, M.D., Assistant Demonstrator in Anatomy, Trinity College, Dublin, proposed by E. Barclay-Smith, G. D. Thane, F. G. Parsons. H. BATTY SHAW, M.B., B.S., F.R.C.S., Demonstrator of Anatomy, University College, London, proposed by G. D. Thane, P. Flemming, F. G. Parsons. J. H. COOKE, M.B., B.S., F.R.C.S., Assistant Demonstrator of Anatomy, University College, London, proposed by G. D. Thane, P. Flemming, F. G. Parsons. *Honorary Members*:—WM. WALDEYER, M.D., Professor of Anatomy in the University of Berlin. W. HIS, M.D., Professor of Anatomy in the University of Leipzig. H. LEBOUcq, M.D., Professor of Anatomy in the University of Ghent.

Dr BARCLAY-SMITH showed the following specimens:—

(1) *An Egyptian skull*, probably female, exhibiting marked asymmetry. The skull was nearly microcephalic, and presented unilateral absence of the coronal suture. The asymmetry was not in accordance with typical plagiocephaly; and whether the unilateral absence of the coronal suture was the determining factor, or merely a concomitant of the condition, was a matter of doubt.

(2) A remarkable case of *dilatation of the Sigmoid Colon*, accompanied by extreme displacements of the stomach, liver, and bladder.

A description of this case will be found on p. 341 of the *Journal of Anatomy and Physiology*.

VARIATION IN THE VERTEBRAL COLUMN OF *LEPUS CUNICULUS*. By GEORGE P. MUDGE, Royal College of Science, London.

HUMPHRY¹ long ago called attention to certain facts suggestive of the double nature of the centrum in the human vertebral column, such as the existence of two nuclei in the odontoid process; the presence of two blood-vessel foramina; and frequently a superficial groove or notch on the forepart of the vertebral body. He cites an instance of cervical spina bifida which he had examined in the museum at Berlin, in which he found several vertebral bodies consisting of two halves, with an opening between them, through which a communication was established with a space in front of the column. In another specimen there was a similar condition of the vertebral bodies in the back. Albers² cites another instance of the same kind.

Müller, according to Humphry, in his *Handbook of Physiology*, says: "the form of the centre of ossification of the body of a vertebra is bilobed; only in the sacral vertebra of a bird have I ever seen it in the form of two distinct ossifying points." Froriep,³ in his paper on the developement of the Chick and Calf, gives several figures which show the bilobed nature of the developing centrum. (See plate 2, figs. iv⁵, and v³, and iv⁴.)

In the museum of the College of Surgeons, according to Humphry, is a specimen of malformed foetus, with the lower part of the spine cleft in twain.

Otto,⁴ Sandifort,⁵ and Bland Sutton⁶ have recorded the deficiency of one-half of the centrum, the two former for Man and the latter for the Rabbit, and Sandifort further mentions the existence of two distinct nuclei in the lumbar vertebræ of a human subject in whom one-half of the centrum was missing in the 7th cervical and 9th and 11th thoracic.

In the *Proceedings* of this Society for November 1891, Howes described a rabbit's backbone in which only one-half of the centra of the 8th and 9th thoracic vertebræ was represented, and in which the left half of the 8th had become confluent in an oblique manner with the right half of the 9th.

One of the vertebræ now exhibited is the 12th thoracic of a young rabbit, in which the centrum is composed of two distinct pieces, and in which the epiphyses occupy a peculiar position. In fig. B, the vertebra is represented from the ventral surface; and it is there shown that the two pieces (c) which compose the centrum are separated from one another by a bony tract, which is continuous on both the anterior and posterior surfaces with an obliquely arranged bony plate, e.

¹ Humphry, *The Human Skeleton*, Cambridge, 1858.

² *Atlas der Path. Anat.*, Bonn, 1847.

³ *Archiv. für Anat. und Phys. Anat. Abth.*, 1886.

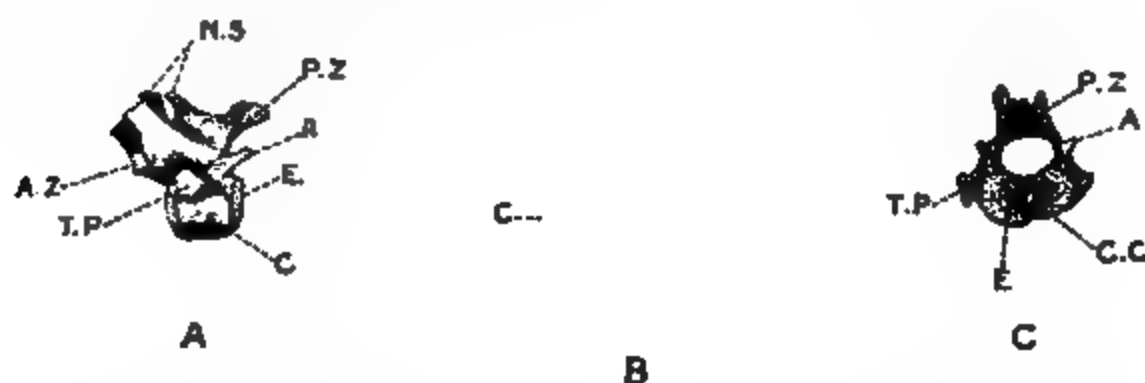
⁴ *Seltene Beobachtungen*, 2te Sammlung.

⁵ Quoted by Humphry.

⁶ *Journ. Anat. and Phys.*, vol. xxiv. p. xv.

When viewed from the posterior surface, fig. C, this plate of bone is seen to completely cover the centrum, and to be perforated by a small central canal. It is worthy of notice that this plate is not composed of a single piece, but of two, the line of demarcation being indicated by a faint division running in a vertical dorso-ventral plane, in front and behind the central canal. Of this division, that portion which lies ventral to the central canal, figs. B and C, is almost completely obliterated by fusion of the two bones, while that lying dorsally is quite apparent. The central canal is thus bounded by two pieces of plate-like bone, which are strongly bent, the summit of the convex surfaces meeting in the dorso-ventral plane above mentioned. The concave surface is directed laterally and dorsally, and within the concavity (figs. A and B) there lies a small bone, *c*, flattened from before backwards, but conical, in a plane which passes from side to side, its apex being outwardly diverted.

When we endeavour to interpret these structures, we are met at the outset with several difficulties, for the two small bones marked *c*



may indicate one of two conditions: we may either regard them as representing two centres of ossification in the centrum which have failed to meet, or we may look upon them as indicative of the confluence of two vertebrae, in each of which only one-half has developed. Variations previously recorded, and to which attention has been called, equally support both views, and we are no nearer a conclusion when we examine other features of the vertebra. It has long been known that chondrification of the centrum proceeds from two centres, and ossification, so far as is known, from one. Upon comparison with Froriep's figures,¹ it appears that these two small bones are coincident in position with the two centres of chondrification; and if this be so, then these two structures represent two bones which have ossified from the same centres as their cartilaginous antecedents. On the other hand, there are several facts which militate against such a conclusion, and will be mentioned later.

The interpretation of the other structures, viz., the two plate-like bones marked *e*, presents even greater difficulty. From their position on either surface of the centrum, which they completely hide, and from the fact that the epiphyses of the vertebra next in front and be-

¹ *Loc. cit.*

hind were in contact with them, it would appear that they represent in part the epiphyses of the vertebra in question. Unless this be the explanation, the epiphyses of this vertebra are absent, for they are otherwise unrepresented. If such is the correct interpretation, the fact that each epiphysis is split in half, the right half of the epiphysis of the anterior surface being continuous with the right half of the posterior (fig. B), and similarly for the left half, seems exceedingly strange. The arrangement of the epiphyses can be to some extent explained by supposing that we have two halves of two adjacent vertebræ which have become confluent. Corroborative of such assumption are the facts that there are only six lumbar vertebræ instead of seven, that the parts of the right side, such as the zygapophyses and metapophyses, are in advance of those of the left (figs. A and B), that there are two neural spines (fig. A), and that the transverse process of the left side is larger than that on the right (fig. B). Such an interpretation, however, involves the further assumption that the epiphyses of the posterior surface have united with the corresponding ones on the anterior surface, but for this I could find no evidence.

The obliquity of the parts of the two sides and presence of two neural spines, however, is not confined to this vertebra alone, for on the ninth, tenth, and eleventh thoracic and the first lumbar the zygapophyses and the metapophyses of the right side are in advance of those of the left, this being more marked in the eleventh than in the others, the eleventh also bearing two neural spines. In these vertebræ there is no indication whatever of confluence of two halves of adjacent vertebræ. It may be, however, that in these the obliquity has been brought about as a matter of adaptation to the altered condition of the twelfth.

On the whole, perhaps, the evidence favours the conclusion that we are dealing with a last thoracic vertebra which has become confluent with a first lumbar, only half of each vertebra having developed rather than with a vertebra the centrum of which has ossified from two centres.

The other two variations I have to record likewise concern the last thoracic, and belong to the vertebral columns of two rabbits in the teaching collection of the Regent Street Polytechnic.

Both are instances of ribs which have become permanently ankylosed with the vertebra; but as the two offer some differences, it will conduce to clearness to describe each separately.

The first presents several variations from the normal. As a rule, the hypapophysis is confined to the 1st and 2nd lumbar vertebræ; it may, however, occasionally occur on the 3rd,¹ and, according to Darwin,² still more so the last thoracic. In the vertebra now under consideration, the median ridge along the ventral surface of the last thoracic centrum bears a small hypapophysis, almost as large as that on the 2nd lumbar. The right transverse process is large and very

¹ Cf. Nathenius, "Die sogenannten Leporiden," Berlin, 1876, p. 16.

² "Variation of Animals and Plants under domestication," edit. 2, vol. i. p. 127.

much expanded for a last thoracic vertebra, and ankylosed with its free end is a rib measuring 2·2 centimetres, possessing a broad expanded head. The rib gradually tapers to a much narrower extremity, and is somewhat slightly bowed, being directed posteriorly and ventrally. Upon the left side, the transverse process is about twice the length of that on the right, but it is flat and expanded in an antero-posterior plane, and in form quite unlike that of the other side. It is about two-thirds the length of the same structure in the succeeding 1st lumbar, and its direction is somewhat different, for it is not directed ventrally to the same extent, and neither is it directed forward at the same acute angle as that. In other respects the vertebra is a typical twelfth thoracic.

The second case presents less variation, the vertebra being normal in all characters, with the exception that the rib of the left side has become firmly and completely ankylosed with the transverse process, which is slightly larger than the corresponding structure of the other side.

[Additional examples illustrating two centres of ossification of the bodies of the vertebræ in man are given by Sir Wm. Turner in the *Challenger Reports*, part xlvii., 1886, and by Professor Reid in *Journal of Anat. and Phys.*, vol. xxi., 1887.]

Professor SYMINGTON gave the results of an examination of the *Thymus in numerous Marsupials*, both pouch specimens and adults, and his paper was illustrated by microscopic specimens and lantern slides of micro-photographs and photographs of dissections. He found that in various examples of the families Macropodidæ, Phalangistidæ, and Phascolomyidæ the thymus consisted of two distinct portions—a thoracic and a cervical. The thoracic thymus presented no unusual characters, but the cervical portion was situated in the ventral part of the neck, covered merely by the skin, platysma, and fascia, and having its deep surface in relation with the sterno-cleido-mastoid muscles and the depressors of the hyoid bone. In many cases the two lateral lobes of this cervical portion extended from the submaxillary gland to the sternum, and they were not connected in any way with the thoracic lobes. The superficial cervical thymus was absent in specimens belonging to the families Didelphidæ and Dasyuridæ.

The paper is published *in extenso* on p. 278 of this *Journal*

Mr E. M. CORNER read a paper on *Notes on the Origin and Development of the Triangular Fibro-Cartilage of the Wrist*. The first part consisted of observations on dissections of the wrist joints of various animals, in which it was shown that the union of the fibro-cartilage and the flexor part of the capsule of the joint became closer as the rotatory movements of the wrist became developed. The development of the fibro-cartilage in the human subject was dealt with. The nodule of cartilage that was described by Professor Leboucq as existing in the radial and palmar part of the triangular

ligament was shown in sections of the third and fourth month foetuses.

It was then suggested that the triangular fibro-cartilage may have arisen as follows. With commencing movements of supination from the primitive pronate condition, a tendency to fasciculation will be established in the capsule round the inferior radio-ulnar joint, on account of the lateral thrust the ulna receives from the radius. These bands are attached to the styloid process of the ulna, and so, with increasing rotatory movements, will be drawn into the joint. Hence the fibro-cartilage may have arisen from the flexor and extensor parts of the capsule, the centre being formed either by coalescence of these parts or by the synovial membrane alone. In support of this double origin, the following facts are well urged:—

1. The relative development of the fibro-cartilage with that of rotatory movements, as seen in the animal series.

2. The gradual absorption into the substance of the fibro-cartilage of two ligaments in the flexor part of the capsule, with the gradual acquisition of rotatory movements, as seen in the animal series.

3. The structure of the ligament, in consisting of flexor and extensor fibrous bands, and a softer cellular structure at the centre.

4. The extreme thickness of the radial part of the triangular ligament at its centre, as seen in sections of the wrist of a 5th month foetus.

5. It accounts for the frequent perforation of the fibro-cartilage in perfectly healthy joints, which especially occur at the radial and central part of the ligament, as an error in its development, or at least as arising from causes predisposing thereto. The elements that appear to make up this structure are:—

1. The two bands of the capsule drawn into the joint by rotatory movements;

2. And between them the remains of the cartilage described by Prof. Leboucq.

The paper is published *in extenso* on p. 272 of the *Journal of Anatomy*.

Professor MACALISTER exhibited a number of skulls showing the three varieties of the anterior nasal spine, for which he suggested the names *oxyacanthic*, *lophacanthic*, and *cryptacanthic*. He showed also a number of varying forms of the *apertura pyriformis*. In these the varieties of the lower border depended on the relative positions of the lateral margin, the paraseptal line passing backwards and outwards from the nasal spine, and the anterior dental ridge which contains the canal for the anterior superior dental nerve and artery. Specimens were also shown illustrating the relations of these ridges to the soft parts both in the European and Australian head, in the foetus and in the adult. When the foetal condition of separateness of the lateral margin and paraseptal line persisted, the blunt-edged aperture may be named *amblycraspedote*; when the two lines united to form a sharp border, the opening may be called *oxycraspedote*, as in the most of

European adults ; when the lateral margin is continued inwards above the incisor alveoli to bound a prenasal fossa, as in Polynesian, the variety may be named *bothrocraspedote* ; and when the nasal floor and the alveolar facial surface are continuous, not separated by a ridge, as in many of the black races, the form may be called *orygmo-craspedote* on the middle area, but so close to the septal ridge that the intermediate area is reduced to a minimum. It is, however, seldom quite abolished, so that the presence of a middle area may be regarded as the characteristic mark of the foetal *apertura pyriformis*.

The paper is published on p. 223 of the *Journal of Anatomy and Physiology*.

PROCEEDINGS OF THE
ANATOMICAL SOCIETY OF GREAT BRITAIN
AND IRELAND.

FEBRUARY 1898.

A GENERAL MEETING of the Society was held at the London Hospital on 2nd February 1898, at 4 P.M. Professor MACALISTER, the President, was in the chair; eighteen members and thirty visitors were present.

Mr KEITH exhibited *the Abdominal and Thoracic Viscera of fourteen bodies* which had been hardened *in situ* by injecting the bodies with a solution containing formalin. Five of the bodies were injected as they lay on the back, two as they lay on the left side, two on the right side, two on the face, two upright with the feet down, and one upright with the head down. Drawings of the bodies, with the organs *in situ*, were also shown. The investigation was made to determine how far organs changed in shape with a change in the position in which the subject was hardened. The most marked change was observed in the viscera of the subjects hardened on the left side. The characters of the viscera of the other bodies, due to the position in which they had been hardened, were not so marked, and were difficult to distinguish from variations which may, and frequently do, occur in bodies which have been hardened in the usual position, on the back. It was necessary, in order to eliminate the great amount of individual variation, to investigate a much larger series of bodies, the present exhibition being merely a preliminary one. A fuller account of the methods used are given in the *Journal*, April 1898, p. 451.

Mr Keith then exhibited *the Abdominal and Thoracic Viscera of an Orang* which had been hardened *in situ* by the injection of formalin. He pointed out the exact correspondence in shape and markings of the liver of the orang to that of the child. A liver of a child, which he put alongside for comparison, showed the same bifurcated lower end of the Spigelian lobe as the orang's. The hepatic artery runs through the notch between these divisions of the Spigelian lobe.

The spleen, which was unfortunately enlarged by tuberculosis, was also of a form frequently seen in human bodies. The upper or third lobe was not well marked in this specimen. The cæcum, the appendix, and ileo-cæcal valve were all exactly of the form seen in the child. The pancreas had a separate duct for its small head, and a very large tail, flattened against the kidney and lower half of the spleen. This part of the pancreas was not transverse, but bent sharply from the body down towards the caudal pole of the kidney. There were four sharply-marked ridges seen in the mucous membrane of the œsophagus. The stomach showed a constriction at the junction of the pyloric and cardiac parts, corresponding to the constriction so frequently seen in human stomachs. The lungs had the same impressions and markings as the human lung; they were, however, of greater width and less in height. Curious processes or buds, such as may be seen in the lung of the human fœtus, filled small recesses in the intercostal spaces between the heads of the ribs. The kidney showed a division into four imperfectly separated pyramids.

A Case of a Supernumerary Lobe of the Right Lung. By Mr A. L. MATTHEWS, introduced by Dr KEITH.

The body in which this abnormality occurred was that of a woman aged 36, and was brought into the dissecting-room of this (the London) hospital in November 1897. The cause of death was carcinoma vulvæ. The lungs were quite healthy, and there were no adhesions between the pleuræ.

The abnormality consists in a lobe of the right lung being cut off from the general substance of the normal upper lobe of the right side by the vena azygos major. This extra lobe includes the apex of the lung, and projects higher up into the neck than the rest of the lung. It is somewhat pyriform in shape, and its constricted neck is encircled behind, outside, and in front by the vena azygos major, which is contained in the free edge of a duplicature of the pleura, which descends from the highest part of the parietal pleura in a vertical direction. In addition to this extra lobe, the lung shows the usual three lobes, though the middle lobe is somewhat smaller than usual.

On the inner side the accessory lobe, in its sac of pleura, is in relation with the trachea, œsophagus, recurrent laryngeal nerve, and the bodies of the upper four dorsal vertebræ. Behind, it rests on the heads of the upper four ribs, and the reflection of the pleural fold from the posterior wall is about half an inch from the heads of the ribs.

The measurements of the cul-de-sac of pleura containing the additional lobe are:—the depth of the cul-de-sac = $2\frac{1}{2}$ in.; depth of the outer sac from the free edge of the duplicature = 2 in. The cul-de-sac, therefore, rises half an inch higher than the rest of the pleura. The size of the aperture of the cul-de-sac:—antero-posterior diameter = $1\frac{3}{8}$ in.; transverse diameter = 1 in. The pleura rises $1\frac{1}{2}$ in. into the neck, above the inner end of the first rib.

The disposition of blood-vessels and bronchi at the hilum of the lung is normal, except that an additional branch from the pulmonary

FIG. 1.—I, first rib; VII, seventh rib; A, vena azygos major in free edge of duplicature of pleura; S, superior vena cava; P, pleura; P', portion of same turned back over sternum; P'', duplicature of pleura. The dotted line represents the height to which the accessory lobe rises in the neck.

artery to the highest lobe in this case crosses over the sparterial bronchus, and reaches the lung at a higher level than the bronchus.

The eparterial bronchus divides into upper and lower divisions. The supernumerary lobe is supplied only by a part of the upper division. This division splits into ventral and dorsal branches. Each branch again divides into upper and lower parts. The upper part of each branch is distributed to the accessory lobe, while the lower part goes to supply the upper part of the normal upper lobe.

I have been able to find the following twelve previously recorded cases:—

1. J. Chiene, in June 1869 (*Jour. of Anat. and Phys.*, iv. 89–90), described “a supernumerary lobe, lying between the upper lobe of the lung and the bodies of the dorsal vertebræ,” in all respects similar to the present. The measurements of the cul-de-sac of pleura in this case were 3 × 2 in.

2. Professor Cleland recorded a case in May 1870 (*Jour. of Anat. and Phys.*, iv. 200).

3. E. W. Collins, in April 1874, *Trans. Roy. Irish Acad.*, and in *Jour. of Anat. and Phys.*, viii. 388.

4. L. Fürst, in 1878; in an article “Missbildungen der Lunge” (*Handbuch der Kinderkrankheiten*, ii. 553–591), alludes to Rokitsansky’s case, the earliest on record.

5–7. W. Allen, of Glasgow, in 1882 (*Jour. of Anat. and Phys.*, xvi. 605–614), reports that between 1877 and 1882 “three well-marked specimens of the lobe have been met with in this medical school. In one case it was present in a foetus, in the others in the adult, and all were in every respect similar to those already put on record.” In one case “the lobe was larger than in the other cases, being made up of the whole of the apex of the right lung; and the sulcus, which cut it off, was horizontal, and not oblique.”

8. A. E. Maylard, in October 1885 (*id.*, xx. 34–38).¹

9–12. Wenzel Gruber, in 1866 (*Arch. für Path. Anat.*, etc., Berlin, ciii. 484), records a case in a man 30 years old. He also reports having seen three other cases—two in new-born children, one in a 13 years old female. Two of these cases he recorded in 1870 (*Bull. de l’Acad. Imp. des Sc. de St Petersburg*, vii. 343–350), the third in 1880 (*Arch. für Path. Anat.*, lxxxi. 475).

During the last three winter sessions 112 bodies have been dissected in this college, and the present case is the only one out of that number in which the supernumerary lobe has been found.

In recording the abnormality, several explanations have been put forward. Professor Cleland gives the explanation, with which E. W. Collins agrees, that at an early period of development there may have been a slight adhesion of the lung to the thoracic wall, or, less probably, an undue curvature of the embryo, and that this has caused the great azygos vein to drag down a fold of the pleura and deeply notch the lung instead of slipping behind both, when the descent of the heart caused the vein to assume a horizontal position, at right angles to its original direction.

Maylard remarks that this explanation tends to class these cases

¹ See also Cruveilhier, *Traité d’Anat. descript.*; 3rd edit., 1852, p. 491.

rather with those where an extra lobe is due to subdivision of a primary lobe, than to the development of an additional one, as was originally supposed.

A consideration of the distribution of the bronchi to the viscus in the present case seems to strengthen the opinion that the lobe is due to the subdivision of a primary lobe; for the eparterial bronchus is seen to divide into two divisions before reaching the lung, and the upper division is distributed, as already described, partly to the accessory lobe and partly to the normal upper lobe.

In the process of development "the jugular vein, coming from the head, and the cardinal vein, coming from the rump (Wolffian bodies), unite on the dorsal side of the cephalic end of the pleural cavity into a single stem, the ductus Cuvieri (the future vena cava superior), which passes in the somatopleure around the outside of the pleural cavity to join the other veins in the dorsal part of the septum transversum" (Minot). Thus, in an embryo of three or four weeks, the duct of Cuvier passes transversely inwards and ventralwards across the neck of the down-growing bud which gives rise to the lungs (figs. 3 and 5). Normally, the bud grows right down internal to the duct of Cuvier, forming only the trachea in this part; and thus, when the lobes of the lung begin to be formed, they grow up external to the vein, which thus comes to arch simply over the root of the lung. If, however, the pulmonary stalk begins to bud earlier than usual, and slightly above the level of the duct of Cuvier, this lobe, or a portion of it, may be cut off by the vein, and prevented from reaching the general pleural invagination on the outer side of the duct (figs. 4 and 6). Thus the vein will be kept away from the middle line of the body, and will encircle the neck of the accessory lobe, which will carry the pleura up with it internal to the vein, thus forming a separate cul-de-sac and a mesentery for the vein. As the lung continues to grow, the root of the accessory lobe will be carried down below the level of the vein, and thus the vein will be entirely above the level of the root of the lung, but will be kept away from the middle line of the body by the portion of lung substance which it constricts. Such, I believe, to be a possible explanation of the formation of the accessory lobe. Though, in the present case, the lobe is evidently formed at the expense of the upper primary lobe, it would seem that in some cases it may be quite separate from the rest; for Chiene distinctly remarks, "this lobe was additional, not formed at the expense of the primary lobes."

Works on comparative anatomy do not seem to throw any light on this formation. Owen, in describing the lobation of the lungs of different kinds of animals, mentions cases where the right lung consists of four lobes in addition to the azygos lobe, but says nothing about the condition of the vena azygos major in any of these cases. Allen reports finding a portion of the upper lobe of the right lung in a porpoise, constricted by the vena azygos major, but there does not seem to be any other recorded case of a similar condition in animals.

With the unusual position of the vena azygos major, the left

superior intercostal vein is enlarged, and drains ten spaces. This is probably due to the blood-flow through the azygos vein being somewhat obstructed by its position, and the communication between the hemi-azygos superior and superior intercostal veins being, in consequence, enlarged.

This specimen, showing the supernumerary lobe, also shows another rather rare anomaly, namely, the suprascapular artery arising from the internal mammary artery.

Professor CUNNINGHAM exhibited an *Occipital bone* which presented an interesting abnormality (fig. 2). On its under surface and around the foramen magnum there was outlined what appeared to be a pro-atlas, or an additional vertebral element. The articular surfaces were

FIG. 2.

distinctly condyloid in character; and the transverse processes, which were feebly marked, formed distinct and separate free projections. The posterior arch of this extra vertebra stood out in relief as a curved ridge, which encircled the foramen magnum behind the condyles. Professor Cunningham stated that he possessed two other skulls, both with paramastoid processes, which showed a somewhat similar condition, but in a much less marked degree. One of these he also exhibited to the Society.

Abnormal Spleen. By ARTHUR LATHAM, M.A., M.B. Oxon., M.R.C.P., Assistant Physician, Victoria Hospital for Children, and Curator of Museum, St George's Hospital, and F. JAFFREY, F.R.C.S., Surgical Registrar, St George's Hospital.

The specimen was removed at the post-mortem examination of a man aged 34, who died from Bright's disease.

The spleen itself is normal, both in position and in shape, but has a tailed process, 13 inches long, which commences in the spleen internal to the hilum, and stretches down to the upper part of the left testis, to which it is firmly attached. The process is thicker at either end, being about the size of a little finger at its upper extremity, and expanding to about the size of a thumb at its lower end. Between these two points it is much smaller, and where it lay in the inguinal canal it is practically a new cord. Both the inguinal canal and the internal and external rings were patent. The process has been submitted to microscopical examination, both in its upper and lower portions: it consists of splenic tissue, with a thickened capsule and excess of fibrous tissue, this excess of fibrous tissue being especially marked at the lower portions.

There was a small congenital hydrocele present.

Mr W. H. Bennett, F.R.C.S., has kindly given me the notes of a similar spleen, which he dissected when demonstrator of anatomy at St George's Hospital in 1873. The spleen was of normal size, but 1-2 inches lower than usual. Its inferior extremity rapidly tailed off to a thin flat process, which, an inch after its commencement, expanded into a rounded mass of ordinary splenic structure. From this the tail-like process passed down through the inguinal canal, and finally terminated a short distance above the testicle. The spleen itself was more irregular than usual, and there were several small accessory splenic nodules lying close to its mesial aspect.

Absence of Gall-Bladder. By ARTHUR LATHAM, M.A., M.B. Oxon., M.R.C.P., Assistant Physician, Victoria Hospital for Children, and Curator of Museum, St George's Hospital.

This specimen was removed at the post-mortem examination of a man aged 49, who died from pulmonary tuberculosis.

There was nothing of any interest in his previous history.

The main point of interest about the specimen is that, in spite of the absence of the gall-bladder, the hepatic ducts are normal, and there is no dilatation of the bile ducts.

Dr T. H. BRYCE exhibited a specimen of an *Extensor Minimi Digiti*, the ulnar slip of which had acquired an attachment to the base of the fifth metacarpal bone. The muscle ended in two tendons in the lower third of the forearm. These passed together through a special compartment of the posterior annular ligament, and immediately thereafter separated. The radial slip was continued forwards, and, after being joined by a slip from the tendon to the ring-finger, formed

the dorsal expansion of the little finger; the ulnar slip was attached to the base of the fifth metacarpal bone. The special interest of the specimen depended on the similarity to the arrangement of the peroneus tertius in the lower extremity.

Dr BARCLAY SMITH exhibited a *Skull* with a remarkable, and, he believed, hitherto undescribed anomaly of the *Malar bone*. On the left side the malar was bipartite, a condition which has been frequently observed. On the right side, not only was the bone bipartite, but the two portions, superior and inferior, were separated from one another by a backward extension of the maxilla, which articulated with the zygomatic process of the temporal.

An intra-jugal temporo-maxillary arch, viz., on the cranial aspect of the malar, has been described by Gruber and others, while the much

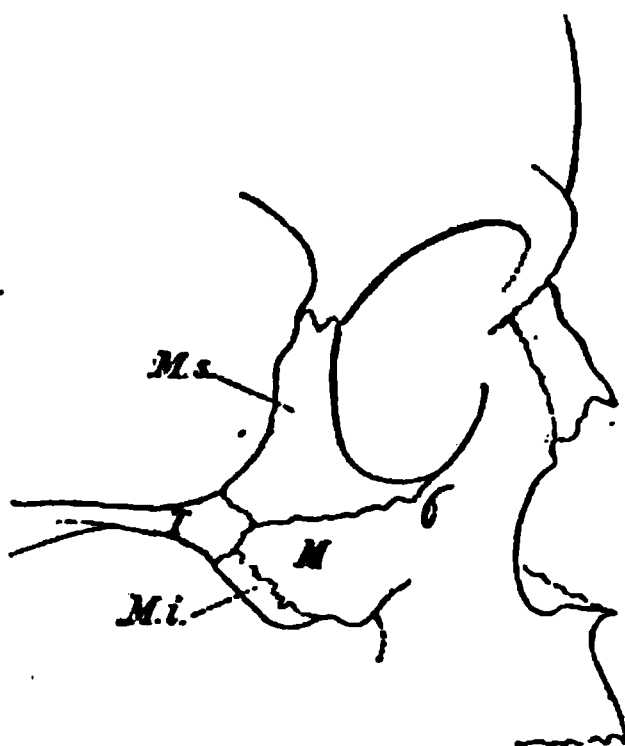


FIG. 3.—T, Temporal; M, Maxilla; M.s., Superior molar; M.i., Inferior molar.

rarer condition of an infra-jugal arch was first recorded by Dieterich, and lately by Romiti.

The case now under consideration might be defined as inter-jugal, and constituted a third and new variety of temporo-maxillary arch.

Professor A. M. PATERSON read a paper on *The Genito-Urinary Organs of the Female Indian Elephant*, in which the results of his own observations were carefully compared with those of other writers on the subject.

The paper is printed *in extenso*, p. 582 of the *Journal of Anatomy*.

Professor CUNNINGHAM read a paper on *The Intrapontine Course of the Seventh Cranial Nerve in Man, the Orang, and the Chimpanzee*, and illustrated his observations by sections through the pons Varolii of each, and by a model which he had constructed of the nerve as seen in the orang. He pointed out that in the orang the nucleus of origin is relatively larger than in man, and that the root-fibres appear to be much more numerous.

Note on the Curvature of the Stomach and Duodenum. By W. J. YOUNG, Univ. Coll., Liverpool. Communicated by Professor PATERSON.

The facts which form the subject of this note are not contained in any of the works on anatomy I have been able to consult, and seem to present features of anatomical and embryological interest.

As usually figured, the lesser curvature of the stomach is represented as continuous with the outer border of the second part of the duodenum, and the greater curvature with its mesial border. In such a figure the antero-superior surface of the stomach is shown as continuous with the anterior surface of the duodenum in both its first and second parts.

Examination of a number of cases leads me to believe that the lesser curvature of the stomach, if carefully traced onwards, is found

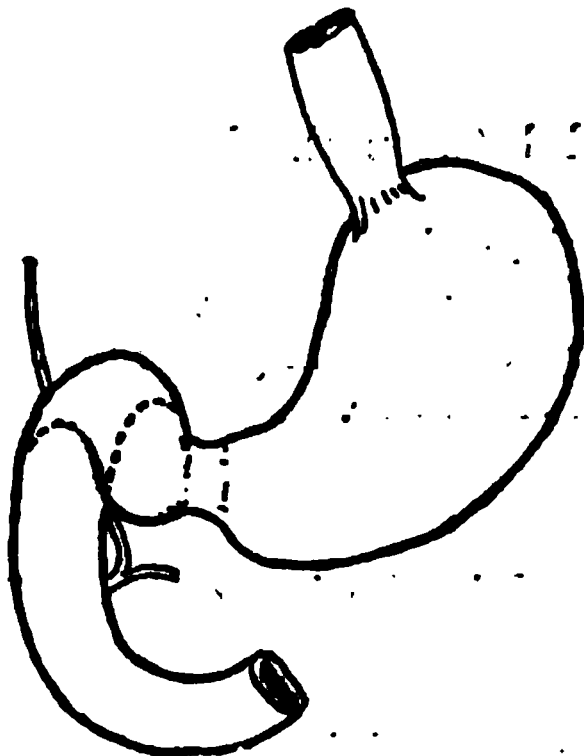


FIG. 4.

to become continuous with the mesial border of the second part of the duodenum, and the greater curvature with the convexity of the duodenum (fig. 4).

The obvious effect of such an arrangement of the borders is that the superior and inferior surfaces of the stomach are continuous respectively with the posterior and anterior surfaces of the second part of the duodenum. This disposition of parts is clearly indicated by a figure in *Gray's Anatomy*, which represents the abdominal viscera with the stomach turned up.

In some cases this feature is not so well marked as in others, but in all the continuity of the lesser curvature of the stomach with the mesial border of the duodenum in its second part was quite evident.

In consideration of these facts, a point of difficulty arises upon which I do not feel competent to enlarge. A striking feature of the anatomy of this region is that the bile duct, originally ventral to the duodenum, lies behind and to the inner side of its second part, and

unites near its orifice with the duct of the pancreas. The question at once occurs, "How has this change in position of the bile duct and pancreatic duct been brought about?" Might it not be suggested that in the embryo some inequality of growth takes place in the duodenum causing a bulging of its wall to the left and forwards, thus bringing the orifice of the bile duct to its right side, and that, later, the duodenum itself falls over to the right? An explanation of this kind would seem at all events to derive a certain amount of anatomical support from the existence of this peculiar twist of the duodenum.

A Persistent Cardinal Vein (Left), with remarks on the neighbouring Veins. By EDWARD FAWCETT.

This condition was met with some time ago in the dissecting-room at University College, Bristol; and as it is a somewhat uncommon one, I venture to record it.

General description.

The vein stretched between the left common iliac and the left innominate veins.

From the former vein, as high as the 8th thoracic vertebra, it was as wide as the little finger; at this level it communicated by a large cross trunk with the vena azygos major, so that the continuation up to the innominate was of small size.

Special description.

This vein commenced in the left common iliac vein, behind the middle of the corresponding artery, and ascended on the internal points of origin of the left psoas magnus muscle, covering the sympathetic cord of that side, and lying to the left side of the abdominal aorta.

It entered the thorax by the aortic orifice of the diaphragm, on the left side of the aorta, ascended in the posterior mediastinum as high as the 8th thoracic vertebra, where it crossed to the right behind the thoracic aorta, and joined the great azygos vein.

At the point where it commenced to cross the middle line it received the trunk formed by the united left superior intercostal and left superior azygos veins, and the former was connected with the left innominate vein by a small pervious trunk, which gave a fibrous cord down to the pericardium, which could be traced to the coronary sinus.

This persistent cardinal vein made the following communications:—

(a) Opposite the 1st lumbar vertebra it communicated with the vena azygos major by a large square branch, whose diameter was $1\frac{1}{2}$ inches. Of this more anon.

(b) Opposite the 8th thoracic vertebra, as has been before said, it entered the great vena azygos; and so large was this communication

that possibly all the remaining blood of the left cardinal system was conveyed to the great azygos vein by it.

The *vena azygos major* commenced in the inferior vena cava opposite the 2nd lumbar vertebra, and it (opposite the 1st lumbar vertebra) communicated by the large square sinus I have already mentioned as lying behind the abdominal aorta, between the crura of the diaphragm with the left cardinal vein.

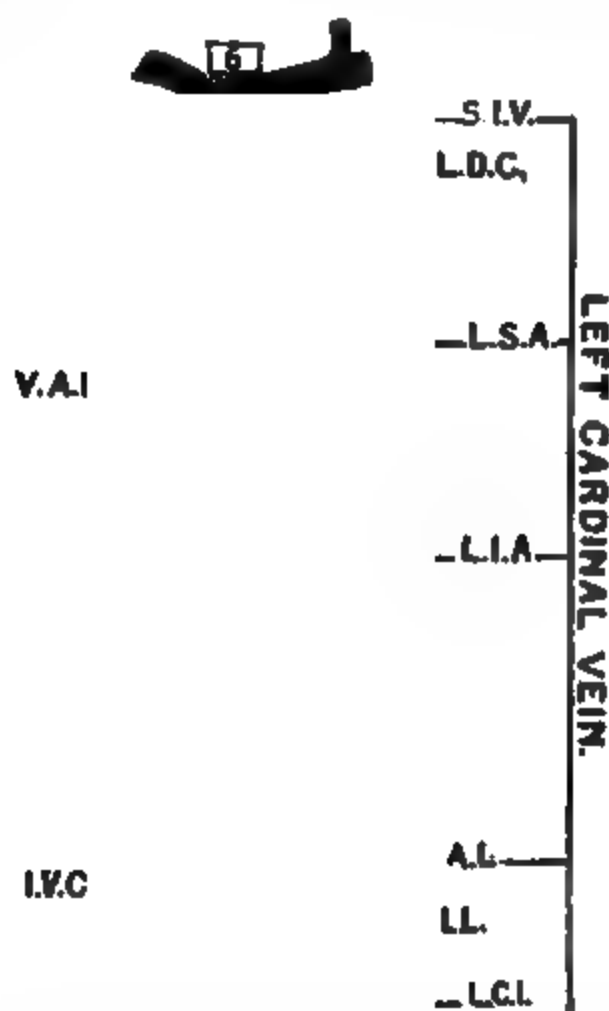


FIG. 5.—S.I.V., left sup. intercostal vein; L.D.C., lower part of left duct of Cuvier; L.S.A., left sup. azygos vein; L.I.A., left inf. azygos vein; R.R., right and left renal veins; A.L., ascending lumbar; L.L., left lumbar veins; L.C.I., left common iliac; C.B., common trunk uniting left lumbar veins and bringing them into communication with inf. vena cava; I.V.C., inf. vena cava; S., right spermatic artery; V.A.M., *vena azygos major*.

This vein having entered the thorax, lay in its usual position, but its calibre was much less than that of the cardinal below the point at which it received the end of that vein.

The *inferior vena cava* was much smaller than usual, as might be expected.

It was formed chiefly by the right common iliac vein, which, opposite the disk between the 4th and 5th lumbar vertebra, received a small transverse branch from the left common iliac and cardinal

junction. In all probability this transverse branch was really the left common iliac vein, much reduced in size.

The inferior vena cava received the right lumbar veins, and a *trunk* which communicated with the left lumbar veins near their junction with the left cardinal vein, and probably drained them of some of their blood. This communicating trunk crossed behind the aorta at the disk between L 3 and L 4.

The right spermatic and right renal vein entered the inferior vena

FIG. 6.—T.A., Thymic artery; V., Thymic vein.

cava (on the left side the spermatic vein joined the renal, as did the capsular).

It is quite obvious how this state of affairs has come about; hence no explanation is necessary from me.

In conclusion, I may say that the left kidney received four arteries, two of which arose close together from the abdominal aorta opposite the 2nd lumbar vertebra, and two opposite the disk between the 3rd and 4th lumbar vertebrae.

A Persistent Thymus.

This somewhat uncommon condition was observed in a female subject aged 28 years, when the sternum was removed in the dissection of the thorax.

As the drawing shows, the gland consisted of two lobes connected by an isthmus. Both lobes, for the greater part of their extent, lay on the front of the pericardium, and they reached *down* to the level of the 4th costal cartilages, upwards over the left innominate vein as high as the thyroid gland, to which they were tied by connective tissue.

Each lobe received an arterial branch, which arose from a stem springing from the inner side of the root of the common carotid artery of the right side; and it is on this account more particularly that the case is mentioned.

The veins from the gland were large, and entered the left innominate.

In the same subject a *musculus supracostalis* was present on the left side, stretching from the 1st rib over the 2nd to the 3rd. It received a nerve from the lateral branch of the 1st intercostal (which was present in this case); the lesser internal cutaneous was absent.

The 2nd costal cartilage was double on this side.

On the same side a deep muscular slip arose from the cartilage of the 10th rib, under cover of the obliquus abdominis externus, and coursed downward, forward, and inwards, to end in the external oblique.

This slip is interesting, perhaps, in association with the supracostalis.

In the same subject a *levator claviculae* was present and a Meckel's diverticulum.

The Eustachian valve was directly continuous with the Thebesian, and there was a patent foramen ovale.

W. H. GASKELL, F.R.S., read a paper on *The Origin of the Cartilaginous Skeleton of Vertebrates*, of which the following is an abstract:—

The author pointed out that the vertebrate cranial skeleton could be referred back step by step to the simple skeleton of the Ammonoetes, in which it is found to consist of two distinct parts: (1) a basi-cranial part consisting of the trabeculae with the parachordals and auditory capsules; (2) a branchial part consisting of a metameric series of branchial bars, which are at first simple and then form the well-known branchial basket-work, and of a pair of longitudinal cartilaginous bars on each side of the notochord, from which at regular intervals the transverse branchial bars spring. These two parts are further characterised, as is well known, by a difference of structure, the basi-cranial skeleton consisting of hard cartilage (the matrix of which stains yellow with picrocarmine and does not stain with

thionin), allied to hyaline cartilage and the branchial skeleton of soft cartilage (the capsules of which stain deep purple with thionin) allied to embryonic or parenchymatous cartilage. Further, this latter cartilage is formed in a peculiar connective tissue called muco-cartilage, which also stains deep purple with thionin.

The author then pointed out that the cartilaginous skeleton of *Limulus* and the Arachnids closely resembled, both in structure and in position, this primitive cartilaginous skeleton of the *Ammocoetes*. Thus in the mesosomatic region each branchial appendage is supported by a bar of cartilage which springs from the entapophysis, and is continuous with the cartilage formed in the two longitudinal entapophyseal ligaments which connect together the series of entapophyses on each side. This cartilage stains deep purple with thionin, is most markedly parenchymatous in character, and is found in a peculiar connective tissue which stains deep purple with thionin, just like the muco-cartilage of *Ammocoetes*. Further, in the prosomatic region the internal cartilaginous skeleton is represented by the plastron or entochondrite which, according to Schimkewitsch, originated as two lateral trabeculae formed of tendinous material. In these tendinous trabeculae nests of cartilage cells are found especially well-marked in the *Thelyphoridae*. The cartilaginous material formed by these cells does not stain with thionin, but stains deep yellow with picrocarmine; it is formed in this white fibrous tissue, which is shown to consist mainly of gelatine, and not in a muco-cartilage, which consists mainly of mucin. The author, therefore, concludes that in both groups of animals a similar mesosomatic or branchial skeleton exists and a similar prosomatic or basi-cranial skeleton; that the cranial skeleton of vertebrates arose therefore in two ways: (1) by the formation of cartilage in a tissue the main substratum of which was a chondromucoid substance, and (2) by the formation of cartilage in a tissue the main substratum of which was a collagenous or gelatinous substance. Finally, he pointed out that there was distinct evidence that one if not both of these internal cartilaginous formations originated from the modification of ingrowths of the external chitinous skeleton, and so an easy explanation was given of the steps by which the internal skeleton of Vertebrates arose from the exo-skeleton of the Arthropod.

